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THE UNIVERSITY OF ALBERTA

FACTORS INFLUENCING THE ENERGETIC EFFICIENCY OF CATTLE

by

© JAMES GEORGE DELFINO

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

IN

ANIMAL NUTRITION

DEPARTMENT OF ANIMAL SCIENCE

EDMONTON, ALBERTA

SPRING 1987

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Date April 15 1987

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ABSTRACT

Factors influencing feedlot performance, energy partitioning and composition of energy gain in cattle fed high-concentrate barley-based diets were measured. In one study, two experiments measured the effects of ionophores on the feedlot performance and energy partitioning. In experiment 1 one hundred Hereford heifers were fed diets containing no ionophore; lasalocid added at 24, 36, or 54 $mg \cdot kg^{-1}$ dry matter (DM); or monensin at 33 $mg \cdot kg^{-1}$ DM for 98 d. Cattle fed lasalocid gained an average of 1.35 kg daily whereas control cattle gained 1.24 kg ($P=.12$). Feed efficiency was improved ($P<.1$) 10% with lasalocid. In experiment 2, four steers were fed the control or lasalocid (36 $mg \cdot kg^{-1}$ DM) diet at 21, 44, 67, and 89 g $DM \cdot kg^{-.75} d^{-1}$. Lasalocid reduced digestible energy loss as methane by 11% ($P<.1$) and improved ($P<.05$) the metabolizable energy (ME) content of the diet by 7%. The ionophore had no effect on the efficiency with which ME was used for tissue gain (kg). Cattle fed lasalocid had decreased ($P<.1$) blood levels of insulin although insulin:glucagon ratios and blood growth hormone levels were unaffected. It was concluded that lasalocid improved feed efficiency primarily by improving the ME content of the diet. In a second study the effects of cold climatic conditions on energy partitioning was investigated with 49 Hereford-type steers in a comparative slaughter feeding trial conducted during the winter. Steers were kept either indoors or outdoors and fed 50, 65, or 80 g

$DM \cdot kg^{-.75}_{d^{-1}}$ for up to 106 days. The daily gains of steers housed indoors were 0.22 kg higher and feed conversion efficiencies were 50% ($P<.001$) better than those kept outdoors. Outdoor steers retained 55% less ($P<.001$) energy than indoor steers. Fasting heat production in the outdoor group was 18% ($P<.01$), efficiency of ME use for maintenance 15% lower, and estimated ME requirements for maintenance 41% higher in the outdoor animals. There was a 41% reduction in kf in the cold environment. In the second study, it was concluded that the main factors contributing to reduced animal performance in the cold were an increased maintenance requirement and a greater proportion of energy being retained as protein.

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I. INTRODUCTION

During the eighteenth century Lavoisier (as cited by Blaxter, 1956) first clearly stated the principles of combustion within the body. His statement that an animal consumes oxygen and combines it with organic substances to give off water and carbon dioxide is still valid today (Kleiber, 1975). In the latter part of the nineteenth century, Rubner (as cited by Blaxter, 1962) demonstrated that the fundamental laws of thermodynamics apply to intact live animal systems. It is these fundamental principles which form the basis of nutritional energetics.

The conventional scheme of energy flow partitions the energy consumed by the animal into various major components. Within this model energy input must equal energy output. Ingested feed energy is partitioned into energy losses (fecal, urinary, gaseous and heat) and energy retained (tissue, milk, eggs and wool). In the ruminant animal the relative proportions of energy which flow into these components is regulated by the physiological and biochemical processes which occur in the animal. In recent years considerable effort has been expended in attempting to understand these processes, how they are influenced by the animal's environment and how they can be manipulated to improve production.

The interaction of an animal with its environment is of particular concern. Of the total livestock production in North America, approximately two-thirds occurs in regions

where the mean midwinter temperature is below 0 C (Young, 1981). The net effect of cold is a decline in the level of production along with a reduction in the efficiency with which the product is formed.

The information on animal performance in cold environments deals mainly with changes in live weight and feed efficiency. Relatively little information is available on carcass characteristics or the partitioning of dietary energy into protein and fat gain in the empty body of animals raised in cold environments. Information on the nutritive value, particularly the net energy content, of dietary components fed to ruminants in cold environments is lacking. Available information indicates that dietary net energy for both maintenance and gain is reduced in the cold (Suleiman and Mathison, 1979). However, interpretation of these results is difficult because measurements were made on different groups of animals and feeds over the experimental periods. Thus more information is needed to further understand the effects of a cold environment on the productive functions of ruminants.

Within the ruminant a major source of variation in digestion is due to the complex inter-relationship between diet, symbiotic microbes and gut physiology. Extensive evidence is available which indicates that this variation may be manipulated by dietary means to regulate fermentation with a view toward improving animal performance (Thomas and Rook, 1980). Initial efforts to achieve improved ruminal

fermentation involved altering the physical form of the diet (ie. grinding, pelleting, wafering, etc.) More recently, chemical additives such as ionophores (Owens, 1982) have been used to manipulate rumen fermentation.

Ionophores act directly to modify ruminal fermentation by selectively inhibiting microbial populations which depend on substrate level phosphorylation for ATP (Bergen and Bates, 1984). This alters the products of fermentation to yield more propionate and less acetate and butyrate. Methane production is reduced also. A decrease in protein degradation in the rumen which allows more dietary protein to bypass fermentation has also been noted with ionophores (Owens, 1980). Ionophores have been shown to have physiological effects on the animal. Decreased turnover of rumen liquids and solids have been reported (Schelling, 1984). This effect in conjunction with the altered microbial population has been postulated to change the extent and site of digestion of various dietary components. The alteration in fermentation together with the physiological effects of ionophores can change the amount of energy available for metabolic processes. This allows the animal to attain the same level of production while reducing feed intake thus improving overall efficiency.

The effects of ionophores on energy partitioning within the animal have not been fully resolved. Garrett (1982) has suggested that ionophores reduce the maintenance requirement of the animal by decreasing fasting heat production. Byers

(1980) has also suggested a decreased maintenance requirement as well as an increase in the estimated dietary net energy values. However little quantative data on these effects are available.

The purpose of these studies was to examine the effects of a cold environment and an ionophore (lasalocid) on energy partitioning of feedlot cattle and to explain how these factors influence the performance of animals.

A. BIBLIOGRAPHY

Bergen, W.G. and D.B. Bates. 1984. Ionophores: Their effect on production efficiency and mode of action. J. Anim. Sci. 58:1465.

Blaxter, K.L. 1956. The nutritive value of feeds as sources of energy: A Review. J. Dairy Sci. 39:1396.

Blaxter, K.L. 1962. The Energy Metabolism of Ruminants. Charles C. Thomas, Springfield.

Byers, F.M. 1980. Determining effects of monensin on energy values of corn silage diets for beef cattle by linear or simi-log methods. J. Anim. Sci. 51:158.

Garrett, W.N. 1982. The influence of monensin on the efficiency of energy utilization by cattle. In: Proc. 9th. Symp. on Energy Metab. Eur. Assoc. Anim. Prod. Pub. 29. pp. 104-117. Lillehammer, Norway.

Kleiber, M. 1975. The Fire of Life, An Introduction to Animal Energetics. John Wiley and Sons, New York.

Owens, F.N. 1980. Ionophore effect on utilization and metabolism of nutrients-ruminants. Proc. Georgia Nutr. Conf. p. 17.

Suleiman , A. and G.W. Mathison. 1979. Net energy evaluation of barley diets for cattle in cold environments. J. Anim. Sci. 48:1447.

Schelling, G.T. 1984. Monensin mode of action in the rumen. J. Anim. Sci. 58:1518.

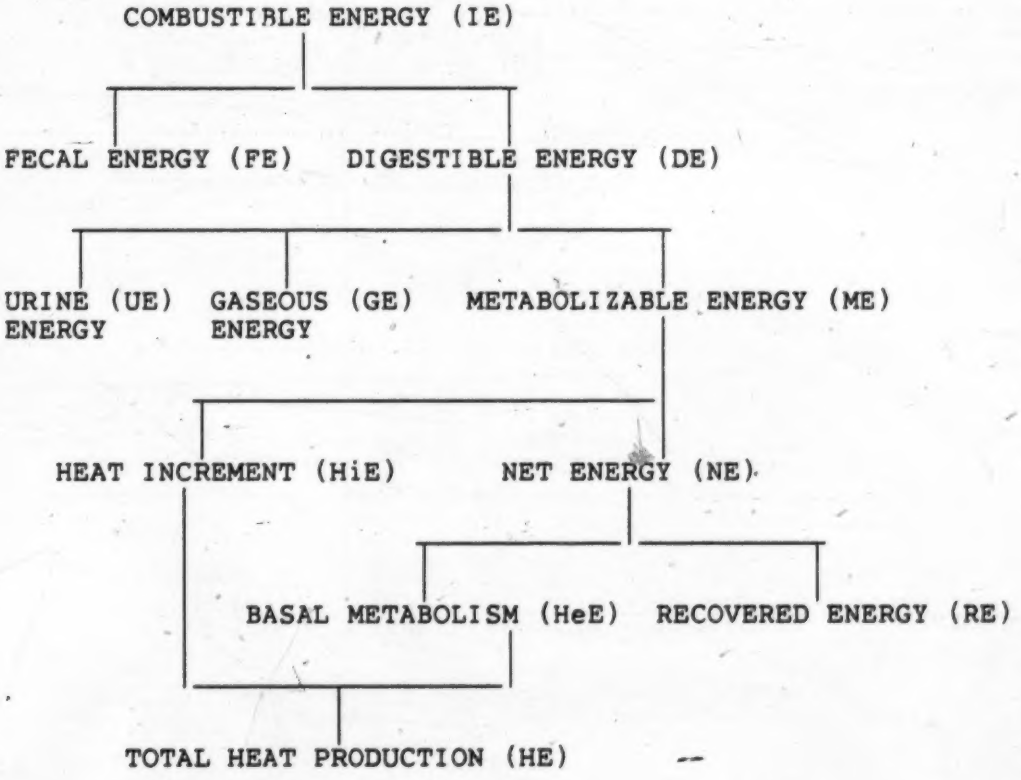
Thomas, P.C. and J.A.F. Rook. 1980. Manipulation of rumen fermentation. In: L.E. Mount (Ed.) Energy Metabolism. p. 157. EAAP Publ. No. 26. Butterworths, London.

Young, B.A. 1981. Cold stress as it affects animal production. J. Anim. Sci. 52:154.

II. EFFECT OF COLD ENVIRONMENTS AND DIETARY IONOPHORES ON ENERGY PARTITIONING IN RUMINANT ANIMALS: A REVIEW OF THE LITERATURE.

A. General scheme of energy partitioning.

The conventional scheme which partitions the energy consumed by the animal into the various major categories is shown below.



The animals source of energy for metabolic functions is derived from its food. The amount of energy ingested (IE) is equal to the combustible energy of the food consumed by

the animal. The energy content of most common ruminant diets averages about 4.4 $kcal \cdot g^{-1}$ dry matter (Garrett and Johnson, 1983). Animals also receive radiant heat energy from exposure to sunlight (Robertshaw, 1985). Although this form of energy does not participate directly in metabolic processes, it can be useful in that it may replace some of the IE which would normally be expended to keep the animal warm in a cold environment. Webster (1971) estimated that the maximum net radiant heat gain during the winter could be as much as 1.84 $Mcal \cdot m^{-2}d^{-1}$ for cattle with access to direct sunlight and overhead shelter at night.

IE is an inaccurate estimate of the energy actually available to the animal because it does not account for the energy losses which occur during digestion and metabolism. Digestible energy (DE) is IE less the energy contained in the feces (FE) which results from the particular quantity of ingested feed. FE losses range from 15% of the IE for corn grain to as much as 60% of the IE in some straws.

Metabolizable energy (ME) is the DE less the energy lost in urine (UE) and combustible gases (GE). Urinary energy losses can vary between 2 and 8% of gross energy (Van Es and Honing, 1979) and tend to be reduced at higher feeding levels.

The GE lost from the digestive tract consists almost entirely of methane. Only under abnormal nutritional conditions are any appreciable amounts of other combustible gases, such as hydrogen, produced (Blaxter, 1967). Methane

energy losses may be estimated to be 8% of IE (Blaxter, 1967). GE losses decline with increasing level of intake above maintenance with the decline being smaller for rations of high digestibility than for those of low. The decline in GE with increasing intake between maintenance and two times maintenance is about 1.0 to 1.5 kcal·100 kcal^{-1} food energy (Blaxter, 1967).

In the process of ingestion, digestion and metabolism of IE, energy is lost as heat in addition to the energy lost in its chemical form in solid, liquid and gaseous excreta. This form of energy loss is referred to as the heat increment of feeding (HiE) and appears over and above the level of heat production represented by basal metabolism (HeE). The main cause of HiE is the energetic inefficiency inherent in the metabolism of absorbed nutrients. Webster (1978) estimated that the work of nutrient metabolism accounts for approximately 70% of the heat increment of feeding. The remainder of the heat increment can be attributed to the energetic cost of eating, ruminating, fermentation and digestion.

Deducting HeE from the ME of a diet gives the net energy (NE) value of the diet. The net energy is that which is available to the animal for maintenance and productive functions. NE for maintenance (NEm) is used to perform work within the body (i.e. blood circulation, enzyme synthesis, maintenance of ion gradients, etc.) and ultimately appears as heat. NE for productive processes (NEg) is stored in the

body as retained energy (RE) or leaves it as chemical energy in a product such as milk or wool.

B. Effects of a Cold Environment.

Effects of a cold environment on animal performance.

Cattle show a marked decline in both the level and efficiency of production when exposed to adverse winter conditions. Chronic cold exposure can reduce feed efficiency 14 to 20% and growth rate may be reduced by as much as 30% in feedlot cattle (Elam, 1970; Webster, 1970; Knox and Handley, 1973; Milligan and Christison, 1974; Ames et al., 1975; Johnson and Crownover, 1975).

Using data involving approximately 40,000 feedlot steers, Ames et al. (1975) predicted the effect of mean ambient temperature (T) on average daily gain (ADG). The relationship was ADG (kg) = 1.369 + .013T over the range 18 to -3 C. This indicates a linear decrease in ADG of .013 kg per degree as temperature decreases.

Milligan and Christison (1974) analysed monthly records, covering seven years, on a total of 1,970 steers from the University of Saskatchewan feedlot at Saskatoon. Their data show that animals fed during the winter required almost 50% more feed and 40% more ME to achieve the same rate of gain as steers fed during the remainder of the year. They estimated that cattle fed during the 90 coldest days of the year required an additional 530 Mcal ME to reach market

weight.

Ingalls and Seale (1967) reported the results of a trial in which Holstein bulls and steers (initial weight, 147 kg) were fed a pelleted 90% concentrate diet ad libitum and housed in a heated barn (10 - 15 C) or in an uninsulated open-front shed. During the coldest part of the trial, December 21 to March 14, feed intake was 12% higher, weight gain 7% lower and feed efficiency 20% lower for the animals in open housing.

Hoffman and Self (1970) investigated the effect of shelter and feedlot surface on performance of yearling steers, fed a 70% concentrate diet consisting of cracked corn and ground corn cobs, during the winter and summer. They reported that shelter in the winter improved ADG by 13% (1.32 vs. 1.15 kg for cattle with and without shelter; respectively) even though feed intake was not different. Similar results were reported by Hidiroglou and Lessard (1971) feeding loose hay ad libitum to steers maintained outside or in a loose housing, closed pole barn. Daily hay consumption averaged 10.8 kg for the outside steers and 10.6 kg for the housed steers. However the outside group had 31% lower ADG (.35 vs. .51 kg for the outside and housed steers; respectively.).

Muhamed et al. (1983) investigated the effect of diet, housing and season on the performance of feedlot cattle. In this experiment a total of 916 steers were fed diets consisting of corn grain and corn silage in ratios of 25:75,

55:45 and 85:15. The housing systems were: outside lots with no overhead shelter, outside lots with overhead shelter and an open-front confinement building. When averaged across all treatments, ADG's were 1.12 vs. 1.05 $kg \cdot d^{-1}$ for summer and winter steers, respectively (7% difference) even though dry matter intakes were similar (8.3 vs. 8.15 $kg \cdot d^{-1}$ for the summer and winter periods, respectively). Overhead shelter had no effect on ADG of steers fed outside during the winter in this trial. In a similar trial Leu et al. (1977) reported that season affected ADG, with cattle in winter gaining 1.07 $kg \cdot d^{-1}$ vs. 1.22 $kg \cdot d^{-1}$ in the summer. In contrast to the study of Muhamad et al. (1983), Leu et al. (1977) found that overhead shelter increased ADG in winter by 9% (1.09 vs. 1.00 $kg \cdot d^{-1}$ for animals with and without overhead shelter, respectively).

Christopherson (1985) summarized the data from 14 trials in which feedlot cattle were fed during the winter and various types of shelter provided. He concluded that providing winter housing for cattle gaining greater than 1.5 $kg \cdot d^{-1}$ may not reduce feed requirements. However for cattle gaining 1 $kg \cdot d^{-1}$, the benefit of an open-front shed was equivalent to a savings of 1.5 Mcal $ME \cdot head^{-1} \cdot d^{-1}$. Providing an insulated barn was calculated to increase the daily energy savings an additional 2.5 $Mcal \cdot head^{-1}$ (Christopherson, 1985).

It is apparent from these studies that cattle exposed to a cold winter environment will have lower feed

efficiencies and reduced overall performance as compared to cattle raised in a warmer environment.

Physiological responses of ruminants to chronic cold environments.

Ruminant livestock are homeotherms and therefore must maintain a relatively constant body core temperature over a wide range of thermal environments (Christopherson and Young, 1986). In order to maintain homeothermy in a changing thermal environment the animal must balance the rate of heat loss with the rate of heat production (Monteith and Mount, 1974; Webster, 1974). This is accomplished by altering the resistance to heat flow, or by increasing or decreasing heat production or by both. The animal can do this by evoking a variety of physiological responses which range from minor adjustments in blood flow and simple behavorial or postural changes to major endocrine and metabolic changes. The degree of the response depends on the effective temperature of the environment to which the animal is exposed and the duration of exposure (Kennedy et al., 1986). The effective environmental temperature is defined by factors such as air temperature, wind, precipitation (rain or snow) and radiation exchange which in combination determine the "coldness" of the environment (Young, 1981). The onset of these physiological responses is determined by the thermoneutral zone (TNZ) and the lower critical temperature (LCT) of the animal (Christopherson and

Young, 1986). The zone of thermoneutrality is defined as the temperature range over which an animal can maintain its thermal balance without appreciably altering its energy expenditure (Yousef, 1985). The lower boundry to the TNZ is known as the LCT and is defined as the minimum temperature which can be tolerated without an acute increase in HE (Christopherson and Young, 1986).

Greater resistance to heat flow in a cold environment can be accomplished by increasing the thermal insulation of the animal. In ruminant animals thermal insulation is provided by the hair coat, the skin and subcutaneous tissue (Young, 1985). Growth of the coat in cattle and sheep is governed by daylight length, the rate of growth increasing with decreasing day length (Webster et al., 1970; Morris, 1961). With sheep, environmental temperature does not appear to influence wool growth (Morris, 1961; Webster et al., 1969) but coat thickness of cattle is affected by temperature (Webster et al., 1970). The latter authors found that the total hair cover was twice as great in cattle wintered outdoors when compared to cattle wintered indoors at thermoneutral temperatures, however there was no difference in growth rate of new hair. They concluded that cold temperatures reduced shedding thus effectively increasing the coat thickness. Webster (1976) has suggested that tissue insulation may be increased as a result of prolonged exposure and adaptation to cold particularly in animals gaining condition during that period. Tissue

insulation may also be increased by vasoconstriction of surface blood vessels and shunting blood away from the extremities (Webster, 1974). For adult cattle, in a thermoneutral environment, the total thermal insulation is estimated to be .35 $C \cdot m^2 \cdot W^{-1}$ (Christopherson and Young, 1986) where C is the temperature gradient between the animal's core and the environment in degrees Celsius, m^2 is the surface area of the animal in meters squared and W is the heat loss in watts. Thermal insulation increases to about .6 $C \cdot m^2 \cdot W^{-1}$ during cold exposure and adaptation (Christopherson and Young, 1986).

Animals adapted to cold environments display an elevated basal metabolic intensity (Young, 1983). Evidence for this phenomenon was reported by Webster et al. (1969) for sheep, Webster et al. (1970) for growing cattle and Young (1975a,b) for adult cattle. In these experiments the animals were initially exposed to a cold environment for an extended period of time. Metabolic rates were then determined when there was no thermal stress on the animal. The results indicated that chronic cold exposure caused an increase in basal metabolism by up to 40% and that the elevation in metabolism lasted for a period of time after the animal was returned to a warm environment. The physiological processes which occur in cold adapted animals and contribute to the elevation in basal metabolism have not been completely resolved. Prolonged cold exposure has been shown to have an effect on several of the hormones which are

involved in metabolic regulation (Sasaki and Weekes, 1986). Christopherson et al. (1978) reported that plasma concentrations of epinephrine and norepinephrine were elevated in sheep during chronic cold exposure. The increase in heat production in response to epinephrine seen in sheep is enhanced by cold acclimation (Graham and Christopherson, 1981). This implies that at least part of the increase in resting metabolism in cold environments may be caused by the action of epinephrine. Plasma levels of thyroxine and triiodiothyronine in cattle and sheep are elevated by cold exposure (Christopherson and Thompson, 1983; Kennedy et al., 1986). Fregly et al. (1979) reported that elevated thyroid hormone levels may potentiate the response to catecholamines in the cold. Gregg and Milligan (1982) reported an increase in the in vitro respiration of skeletal muscle in cold acclimated sheep, particularly that associated with Na^+/ K^+ - ATPase. Sasaki and Weekes (1986) have proposed that this response may be due to the influence of cold induced elevated thyroid hormone levels on mitochondrial structure.

The result of the increase in basal metabolic rate in response to chronic cold exposure is an improved ability to tolerate severe cold stress (Webster et al., 1969; Slee, 1985; Young, 1985) and therefore an improved ability to survive. However, the high rate of heat production which is necessary to confer this protection is an energetic cost (Christopherson and Young, 1986). Christopherson and Young

(1986) have estimated this cost in terms of the increase in resting heat production per degree decrease in adaptation temperature. Their values range from about $0.6\ kcal \cdot kg^{-.75} \cdot C^{-1}$ for growing calves and steers to about $1.0\ kcal \cdot kg^{-.75} \cdot C^{-1}$ for adult sheep. These authors suggest that the response to chronic cold exposure begins with the onset of cold weather and gradually increases in magnitude as the animal adapts to increasingly colder temperatures. Thus the animal's basal metabolism begins to increase at temperatures within the so-called thermoneutral zone (Christopherson and Young, 1986). This is in contrast to the response to acute cold stress in which the basal metabolic rate of the animal is relatively unaffected by short term, abrupt, exposure to temperatures below its lower critical temperature (Yousef, 1985).

A further consequence of adaptation of ruminants to cold environments is a reduction in diet digestibility with declining environmental temperature (Colditz and Kellaway, 1971; Warren et al., 1974; Christopherson, 1976; Westra and Christopherson, 1976; Kennedy et al., 1976, 1977; Kennedy and Milligan, 1978; Nicholson et al., 1980). In experiments with sheep fed long, chopped or pelleted hay (Westra and Christopherson, 1976; Nicholson et al., 1980), digestibility decreased in a linear manner as temperature declined over the range 18 to -8 C. The extent of depression in digestibility of the hay diets was approximately 0.15 to 0.2 percentage units per degree decline in ambient temperature

and was consistent within each physical form of diet.

The magnitude of the depression in digestibility observed in ruminants subjected to declining environmental temperatures appears to vary with the type of diet fed to the animal (Kennedy et al., 1986). When high quality all-concentrate or high-concentrate diets are are fed to ruminants, cold exposure does not induce a depression in digestibility. This was demonstrated by Young and Degan (1981) in two experiments with sheep. In the first study the animals exposed to temperatures of 0 and 30 C were offered a pelleted diet consisting of equal portions of barley grain and dehydrated alfalfa meal at feeding levels of 500 to 1250 $g \cdot d^{-1}$. The authors reported that neither temperature nor feeding level had an effect on diet digestibility. In the second trial sheep were offered 1000 $g \cdot d^{-1}$ of the same barley-alfalfa diet and exposed to a temperature of either 0 or 30 C. Diet digestibility and rate of passage of liquid and solid digesta were determined at each tempeature. The results showed that neither rate of passage of the liquid or the solid portion of the digesta were affected by temperature, and as well, no depression in digestibility was seen (Young and Degan, 1981). Similar results have been reported in other trials where high-concentrate diets have been fed to animals exposed to cold environmental temperatures (Kennedy et al., 1982; McBride and Christopherson, 1984).

The depression in digestibility observed in ruminants exposed to cold temperatures appears to be due mainly to the faster rate of passage of dietary material through the reticulorumen with relatively little effect on post-ruminal retention time of digesta (Christopherson and Kennedy, 1983). Kennedy et al. (1986) summarized the results of several detailed experiments with shorn sheep exposed to ambient temperatures that differed by 20 C (20 - 25 C vs. 0 - 5 C). The decrease in retention time of digesta solids markers in the whole tract of cold exposed sheep ranged from 6.5 h for the pelleted brome grass diet to 0.9 h for chopped brome hay, with values for reed canarygrass hay, alfalfa hay, red clover hay and pelleted reed canarygrass falling between these values.

The relationship between retention time of digesta in the rumen and the rate of digestion of the various dietary components will determine the extent of the depression in digestibility of a diet when it is fed to cold exposed ruminants. Mertens (1977) has shown that, after an initial lag, the digestion of cell wall constituents (CWC) follows a first-order reaction and eventually reaches an asymtotic value. If the time needed to reach this asymtotic value is relatively long, then a reduction in retention time in the cold may significantly influence the amount CWC degraded (Kennedy et al., 1986). An example of this is seen in the data of Kennedy (1985) who measured the disappearance of CWC of four forage diets from nylon bags suspended in the rumen

of warm or cold exposed sheep. His results showed that cold per se did not consistently effect the rate of digestion of CWC from the nylon bags, however, reducing the residence time of the nylon bags in the rumen from 20 h to 10 h decreased CWC digestion by 9%. In vivo measurements using digesta markers showed that cold exposure decreased the retention time of CWC by about 5 h which was equivalent to a 4% decrease in digestibility (Kennedy, 1985). Similar principles apply to the digestion of organic matter (OM), although the presence of readily fermentable carbohydrates and proteins makes interpretation of the results difficult (Kennedy et al., 1986).

The decrease in digestibility of OM and CWC in the rumen of cold exposed animals has been shown to influence VFA patterns and methane production. Kennedy and Milligan (1978) reported that total methane production declined 23% in the cold which was about the same as the reduction seen in OM digestion of the pelleted brome grass diet. Kennedy (1985) reported a decline in the acetate to propionate ratio in cold exposed sheep fed four different hay diets. Total VFA concentration was also reduced an average of 10% and rumen pH was increased by cold exposure. Changes in VFA ratios were also reported by Kennedy et al. (1976), Kennedy and Milligan (1978) and Weston (1983), however, in these studies there was no consistent increase or decrease in total VFA concentrations. Kennedy et al. (1986) have suggested that the changes in VFA proportions are what would

be expected if rumen microbes were less dependent on CWC as an energy substrate in cold environments.

Several physiological factors may be involved in reducing the retention time of digesta in cold exposed ruminants. An increase in the frequency of contractions of the reticulorumen may increase the rate of passage of material out of the rumen (Kennedy et al., 1986). Experiments with sheep (Westra and Christopherson, 1976; Kennedy, 1985) and cattle (Gonyou et al., 1979) given restricted quantities of feed and exposed to both chronic and short-term cold showed an increase in the frequency of biphasic reticular contractions. However, the increased rate of contraction may not be simply related to increased passage of digesta out of the rumen (Kennedy et al., 1986). Freer et al. (1962) reported that the weight of organic matter transfered to the omasum with each reticular contraction in cows varied between 1.8 and 3.6 g. Kennedy (1985) noted that with sheep given pelleted diets, the 10% increase in reticulum contraction frequency in cold exposed sheep was associated with an 18% decrease in transfer of digesta to the duodenum per contraction. Thus the role of gut motility in increasing the rate of passage of digesta through the digestive tract during cold exposure has not been fully resolved.

Decreases in rumen fluid volume with cold exposure have been reported in several experiments and may influence digesta flow to the intestine with each reticular

contraction (Kennedy et al., 1976; Kennedy and Milligan, 1978; Weston, 1983). Kennedy et al. (1986) point out that in the absence of a decrease in feed intake, the decreased rumen fluid volume that occurs in response to cold exposure would necessitate reduced turnover time of digesta and thus a reduction in retention time if equal throughput of material is to be maintained. The cause of the change in rumen fluid volume in the cold is not clear. Kennedy and Milligan (1978) found that changes in saliva secretion rate are not responsible for the change. Young and Degan (1981) suggested that the changes in rumen fluid volume may be related to the decrease in water consumption and body-water turnover in the cold. However, Weston (1983) reported a decrease in rumen fluid volume in cold exposed sheep in spite of a daily infusion of 5.6 l of water into the rumen.

The physical form of the diet and the chewing behavior of the animal may also influence the rate at which digesta leave the rumen in cold exposed animals. Kennedy (1985) reported that when intake was held constant the reduction in digestion of grass hays due to cold exposure was not influenced by the physical form of the diet. However, when feed intake was permitted to increase to ad libitum, during the cold stress period, the consumption of the chopped grass hays increased by 13% while the consumption of the pelleted form remained unchanged. Weston (1983) and Chai et al. (1985) reported that in cold exposed sheep, rumen fluid volume tended to be smaller and rumination time was longer

which could account for an increased passage of digesta out of the rumen thus allowing an increase in feed intake of the chopped grass hay diets.

The increase in voluntary feed consumption (VFC) in ruminants exposed to cold temperatures is well recognized (Baile and Forbes, 1974; NRC, 1984). Webster (1970) reported that heifers increased hay intake by 21% during the coldest part of the winter. Christopherson (cited by Kennedy et al., 1986) has demonstrated that a lag period or delay may occur in the onset of increased feed intake which is dependent on the type of diet being fed. Increased VFC of pelleted hay diets is delayed by approximately two weeks after the onset of cold exposure, while a further two to three weeks may be required for VFC to increase with pelleted roughage-concentrate diets.

In some cases the changes in digestive function with temperature are beneficial to the animal. The increased VFC of the cold exposed animal may allow the animal to maintain a reasonable level of production although at a higher feed cost (Christopherson and Young, 1986). Cold exposure can increase the efficiency of microbial protein synthesis in the rumen and nitrogen recycling (Kennedy et al., 1976; Kennedy and Milligan, 1978). Cold exposure has also been shown to increase the amount of non-ammonia nitrogen escaping the rumen and being digested in the small intestine (Kennedy et al., 1986). These authors reported that for 12 of 14 diets studied the increase in nonammonia nitrogen

escaping the rumen in cold exposed sheep averaged 16% and was independent of feed intake. These beneficial changes in nitrogen transactions may allow the animal to utilize a diet with a slightly lower nitrogen content in a cold environment (Christopherson and Young, 1986). Ames and Brink (1977) demonstrated that sheep could be fed diets with a lower nitrogen content during cold weather.

The adaptation of ruminant animals to chronic cold environments results in increased thermal insulation, metabolic intensity and reduced digestive function. Although these changes are beneficial to the animal in terms of survival, they are costly in terms of production. Much of the reduced performance in ruminant animals raised in cold envirnments can be related to the chronic changes in resting metabolic rate and digestibility of diets associated with adaptation.

C. Effects of Ionophores.

Effect of ionophores on animal performance.

The various ionophores which are used in ruminant diets have been found to have similar effects on animal performance (Owens, 1980). In general, ionophores depress feed intake without substantially influencing weight gains, thus improving feed to gain ratios and overall efficiency.

Goodrich et al. (1984) summarized the performance data of over 11,000 head of feedlot cattle fed control and

monensin supplemented diets and reported that feed consumption was reduced an average of 6.4%. The results of seven trials in which feedlot steers were fed diets supplemented with lasalocid were sumarized by Owens (1980). He reported that lasalocid reduced feed intake an average of 3.2%. In studies where both ionophores were compared, monensin appeared to reduce feed intake more than lasalocid (Bartley et al. 1979; Berger et al. 1981). The reasons for the decreased feed intake are not completely understood, however Baile et al.(1979) have proposed that a malaise is caused by monensin which the animal associates with the odor or flavor of the ionophore. A second cause proposed by Lemenager et al. (1978) is the reduced ruminal function and outflow observed with ionophore supplemented diets. In contrast, ionophores do not appear to affect feed intake when included in high roughage diets (Potter et al., 1976; Thonney et al., 1981).

Weight gains of ionophore-fed cattle are not affected by the reduced feed intake and may be slightly improved compared to control animals when feeding periods are longer than 60 days (Owens, 1980). Goodrich et al. (1984) reported that cattle fed monensin gained 1.6% faster than controls. Owens (1980) reported a 2.6% advantage for lasalocid fed cattle. Weight gains of pasture fed cattle are substantially increased with ionophore supplementation. In 24 trials, monensin supplemented grazing cattle gained 13.1% faster than controls (Goodrich et al., 1984). Spears and

Harvey (1984) reported a 17% advantage in average daily gains for pasture fed cattle supplemented with lasalocid.

The combination of reduced feed intake and slight improvement in weight gain results in a reduction in the feed required per kg gain of 6 to 8% in cattle supplemented with ionophores (Owens, 1980; Goodrich et al., 1984).

Ionophores have been shown to reduce or even eliminate the effects of several feedlot disorders which can have a detrimental influence on animal performance. Lactic acidosis occurs when the diet of ruminants is abruptly changed from forage to concentrates or when abnormally high intakes of concentrates follow periods when stress has caused cattle to reduce feed intake (Goodrich et al., 1984). Under these conditions gram positive organisms are the major producers of lactic acid (Bergan and Bates, 1984). Chen and Wolin (1979) reported that growth of bacteria in pure culture with gram positive cell wall characteristics are inhibited by ionophores whereas Dinnis et al. (1981a,b) have indicated that the ruminal lactate utilizers are not inhibited by ionophores. During in vivo studies designed to induce lactic acidosis in cattle by engorgement with grain or a glucose solution, Nagaraja et al. (1981, 1982) determined that both monensin and lasalocid were effective in preventing lactic acid accumulation thus preventing a decrease in ruminal pH. Further, it was reported that lasalocid appeared to be more potent than monensin in inhibiting several strains of S. bovis as well as depressing

L(+) lactic acid accumulation in in vitro rumen fermentations utilizing rumen fluid from cattle not adapted to high grain rations (Dinnis et al., 1981a,b). Burrin and Britton (1986) reported that monensin supplemented steers maintained a more favorable rumen pH after being switched from a low to a high grain diet when compared with unsupplemented steers. However, in contrast to the previous studies, the decline in pH was due to increased ruminal VFA concentrations on the high grain diet rather than to increased lactate concentrations. Monensin supplementation reduced total VFA concentrations primarily by reducing acetate and butyrate concentrations (Burrin and Britton, 1986).

Another disorder which affects young feedlot cattle, generally between 6 and 8 mo of age, and can cause considerable weight loss thus requiring a longer feeding period is coccidiosis (Fitzgerald, 1975). Several studies have reported that feeding diets supplemented with ionophores, at dosages similar to those used to improve feed utilization, were effective in preventing the clinical signs of coccidiosis after experimental inoculation (Fitzgerald and Mansfield, 1973; McDougald, 1978; Stockdale and Yates, 1978). Monensin has also been shown to be beneficial in the control of face and horn flies (Herald and Knapp, 1980; Herald et al., 1982).

Bloat is another common disorder of feedlot cattle which may respond to ionophores. Despite extensive research

the etiology of bloat has not been completely resolved. The results of numerous studies suggest that plant, host and rumen microbial factors all contribute to the development of bloat. Cheng et al. (1976) have implicated ruminal slime production as a contributing factor to induction of bloat. Ionophores may reduce slime production by inhibiting growth of ruminal protozoa and the gram positive bacteria S. bovis (Bergen and Bates, 1984). Sakauchi and Hoshino (1981) reported that monensin was effective in lowering the incidence of feedlot bloat in cattle, however they could not relate this effect to changes in ruminal protozoal metabolism. The possible role of S. bovis was not considered in this experiment (Sakauchi and Hoshino, 1981).

It is apparent from these studies that ionophores influence the performance of feedlot and pasture fed animals in a variety of direct and indirect ways. Ionophores reduce feed intake, improve ruminal fermentation efficiency and have a protein sparing effect, all of which directly effect the performance of the animal. They also reduce the incidence and severity of certain feedlot disorders which would have a detrimental influence on animal peformance.

Mode of action of ionophores.

Ionophores are chemical compounds of approximately 200 to 2000 molecular weight that are capable of forming lipid-soluble complexes with polar cations. The association-dissociation kinetics and diffusion rates across

lipid barriers determined in physical studies indicate that their transport turnover numbers across biological membranes reach values of thousands per second. This rate exceeds the turnover numbers of most macromolecular enzyme systems (Pressman, 1976) and appears to be the principal mode of action of ionophores in moderating ruminant production systems.

Ionophores are commonly categorized into three classes according to their transport modes: neutral ionophores, carboxylic ionophores and channel-forming quazi-ionophores. The ionophores monensin and lasalocid, which are in common use in ruminant diets, belong to the carboxylic class. The naturally occuring carboxylic ionophores have linear backbones made up of oxygen containing heterocyclic rings (Pressman, 1976). These rings provide a variety of functional oxygen groups for cation liganding. The common feature of a carboxyl group at the head of the molecule and one or two hydroxyl groups at the tail effectively cyclize the molecule through hydrogen bonding (Ovchinnikov et al., 1974). Further stabilization is conferred by twists in the assymetric centers and rings of the backbone (Pressman, 1976). Once cyclized the ionophore assumes a critical conformation which focuses the oxygens about a ring in the center of the molecule. This becomes the active site into which a complexable cation may fit.

Pressman (1976) and Painter et al. (1982) examined in detail the "cation-for-proton" exchange which is mediated by

the carboxylic ionophores. The transport mechanism is characterized as a cycle which begins with the unfilled or anionic form of the ionophore confined to the polar interface of a membrane. On the membrane surface the ionophore is exposed to complexible metal cations (M^+) with which it interacts to form a lipophyllic ionophore - M^+ complex. In this zwitterionic form it is able to break away from the interface and diffuse across the membrane to the opposite interface. There the ionophore releases the metal cation and becomes trapped once again. The anionic ionophore is then able to combine with a proton (H^+), lowering its polarity and permitting it to leave the interface and return across the membrane to the original interface and release the proton thus completing the cycle. This cyclic transport pattern is characteristic of both monensin and lasalocid.

The direction of the "cation-for-proton" exchange appears to be dependent on the respective chemical gradients for M^+ and H^+. Sandeaux et al. (1982) have recently examined the transport cycle for monensin and determined that when Na^+ is taken across a membrane in a 1:1 complex with monensin, the protonated form of the ionophore only, makes the return trip. In the presence of monensin the authors measured the flux of $^{22}Na^+$ ions when the initial pH was the same on both sides of the membrane and Na^+ concentrations varied. They then repeated the experiment holding the Na^+ concentrations constant on both sides of the

membrane and varying the pH (Sandeaux et al. 1982). Their results indicated that when pH was held constant the flux of Na^+ was down its concentration gradient. When pH was varied the transport of Na^+ was opposite to the flux of H^+ ions which moved from the high potential to the low potential side of the membrane. The flux of Na^+ was obligatorily coupled to H^+ transport in the opposite direction even though Na^+ transport was against its own gradient. Haynes et al. (1980) found that lasalocid does not display the same obligatory cation-proton exchange mechanism. They demonstrated an electroneutral exchange of one Ca^{2+} ion for two K^+ ions.

Ionophores complex more readily with certain cations than with others. The apparent affinity constant (k_a) is a measure of the attraction of an ionophore for a particular cation and is equal to the reciprocal cation concentration giving a half-maximal increase in complexation (Haynes and Pressman, 1974). The k_a of lasalocid for monovalent ions ranges from $10^{1.3}$ to $10^{2.0}$ and for divalent ions between $10^{1.9}$ and $10^{3.2}$ (Haynes and Pressman, 1974). Thus the affinity of ionophores for all cations is not the same. The affinity of monensin for Na^+ is ten times that for K^+ therefore monensin mediates primarily Na^+- H^+ exchanges (Pressman, 1976). Lasalocid on the other hand has a higher affinity for K^+, with Na^+ and Ca^{2+} having approximately equal attraction. In the ruminal ecosystem, where cationic concentrations are variable, the apparent concentration

gradient of a cation across a membrane in conjunction with k_a will determine the rate and degree with which an ionophore will transport that particular cation. Thus it is possible, with proper conditions, that several ion gradients could be dissipated simultaneously (Ovchinnikov et al., 1974).

An understanding of the importance of ion flux to both bacterial cells and mitochondria is necessary in order to assess the full impact of ionophores on microbial and host metabolism. The role of ion flux in cellular energetics was put forth by Mitchell (1961) in his chemiosmotic theory of energy transformations in coupled systems. The basis for this hypothesis is that metabolic energy is stored at the level of the membrane as an electrochemical gradient of hydrogen ions. The establishment of an electrochemical gradient requires an intact membrane that is impermeable to protons and a mechanism to move protons to one side of the membrane. The exclusion of H^+ to the outside of the membrane sets up a pH differential as well as a difference in electrical potential across the membrane. The sum of these two components is the proton motive force (PMF). According to Mitchell (1961), PMF is the driving force of ATP synthesis by reversible membrane bound ATPase. The formation of each ATP molecule is accompanied by proton transport across the membrane in a direction opposite to that in which the protons were "pumped" out (Ovchinnikov, 1974).

Two prominent mechanisms appear to be charged with establishment of the proton gradient. The simplest is the membrane bound F0 F1 ATPase which is ubiquitous to all cells (Wilson and Smith, 1979). In this system the F0 portion is the ion channel through which protons leave the cell, and the F1 portion of the enzyme catalyzes the ATP to ADP + Pi hydrolysis which drives the proton pump. This is the primary method of proton extrusion in anaerobes which rely on substrate level phosphorylation to generate ATP. The second mechanism of proton extrusion is by electron transport. The transport of electrons along the carriers of the respiratory chain, which are located in the mitochondrial membrane, result in the extraction of protons from the inside of the membrane and their ejection into the surrounding medium (Mitchell, 1961). The free energy decline occuring in electron transport is thus conserved in the form of a proton gradient across the membrane. Thauer et al. (1977) have shown that electron transport can be coupled to transmembrane proton extrusion in certain bacterial species. These two mechanisms are termed primary active transport systems because they convert chemical energy into electrostatic energy.

A third primary transport system is found in the cytoplasmic membrane of eukaryotic cells (DeVoe, 1974). The Na^+/K^+ ATPase enzyme establishes a Na^+, rather than a H^+ gradient, by translocation of $3Na^+/2K^+$ with the expenditure of one ATP. This enzyme has an important role in such

cellular functions as osmoregulation, excitation and solute transport.

In cells capable of oxidative phosphorylation the PMF stored in the proton gradient is coupled to ATP synthesis. This is accomplished by reversal of the flow of protons through the membrane bound F0 F1 ATPase. The inflow of H^+ through the F0 portion supplies the necessary energy to catalyze the generation of ATP from ADP and Pi by the F1 part of the enzyme.

Coupled to these primary active transport systems are the secondary active transport systems. These secondary systems couple the energy stored in the ion gradients to active uptake of nutrients against their concentration gradients. This type of coupling is responsible for the uptake of amino acids, sugars and ions (Eddy, 1978; Rosen and Kashket, 1978; Booth and Hamilton, 1980) and has been found in both eukaryotic and prokaryotic cells. The secondary active transport mechanisms may be grouped into three carrier systems (Rosen and Kashket, 1978). Each of the three systems involves a single substrate carrier for translocation across a membrane. The first is the symport system in which two solutes are simultaneously transported in the same direction. One solute is flowing down its concentration gradient and in doing so provides the energy to transport the second solute up its gradient. The second system, called an antiport, also transports two molecules simultaneously, however their translocation is in opposite

directions. The third system, called a uniport, involves the transport of a single molecule. The energy for translocation in this system is derived from the membrane electrical potential when a charged solute is transported. Facilitated diffusion occurs when an uncharged molecule is moved across a membrane in the uniport system.

Ionophores are effectively able to bypass the mechanisms described above and dissipate ion gradients without coupling them to useful functions. Jolliffe et al. (1981) using Bacillus subtilis reported that monensin could totally dissipate the proton gradient across the cell membrane. This caused the intracellular pool of ATP to become totally depleted, reducing the PMF and severely depressing the overall energy status of the cell. Kitada and Horikoshi (1982) reported similar results with alkalophilic Bacillus 8-1. Na^+ gradients can also be dissipated by monensin if the potential stored in them is greater than the potential stored in the proton gradient (Bergen and Bates, 1984). This has been demonstrated in several bacteria dependent on a Na^+ symport for active uptake of cellular substrates (Andu et al., 1982; Kitada and Horikosi, 1982). In these experiments the translocation of L-glutamate, D-glucose and acetate were severely inhibited by monensin.

The Na^+/K^+ ATPase primary transport system in eukaryotic cytoplasmic cell membranes appears to be relatively unaffected directly by ionophores. However,

ionophores can exert indirect influence on the system. This occurs mainly by uncoupling of oxidative phosphorylation in the mitochondria thereby diminishing the intracellular ATP pool (Levinson, 1967; Gordon and de Hartog, 1968).

Rumen bacteria display a large variation in their capacity to generate ion gradients across their plasma membranes. As obligate anaerobes they depend on substrate level phosphorylation coupled to fermentative processes to generate ATP (Hungate, 1966). The ATP is then used by the F0 F1 ATPase to pump protons out of the cell. Therefore an overall expenditure of ATP is necessary to form the proton and Na^+ gradients which are required to drive the secondary transport systems. Some gram negative rumen species also contain an electron transport system which is comprised of membrane bound enzymes capable of extruding H^+ as electrons are passed from donor to acceptor (Thauer et al., 1977) thus generating a proton gradient without expending ATP. Four emzyme systems have been identified which are capable of this: 1) fumarate reductase; 2) nitrate reductase; 3) the system that catalyzes the reduction of CO_2 to methane and 4) the system catalyzing dissimilatory sulfate reduction (Bergen and Bates, 1984).

The degree to which ionophores affect the various rumen organisms is dependent on the primary system used by the microbe to set up its proton gradient. Gram positive organisms which rely mainly on substrate level phosphorylation for ATP synthesis and the utilization of ATP

for H^+ extrusion are seriously inhibited. Gram negative organisms which can utilize electron transport to form the proton gradient are at a selective advantage. In this way ionophores change the microbial ecology of the rumen and as a result alter the ruminal fermentation pattern. The in vitro work of Chen and Wolin (1979) and Wallace et al. (1981) with monensin demonstrate these effects. Their work shows that gram negative strains, many of which produce succinate via the fumarate reductase pathway, are only inhibited slightly by monensin. The gram positive organisms which are the primary producers of acetate, butyrate, H_2 and formate show marked inhibition to monensin. With the increase in gram negative bacteria more carbon and reducing equivalents are shunted to succinate which is in turn converted to propionic acid. This accounts for the shift in the molar proportions of VFA (Bergen and Bates, 1984). The fumarate reductase reaction produces ATP via oxidative phosphorylation, which gives gram negative organisms a further metabolic advantage (Hobson and Summers, 1967, 1972; Reddy and Peck, 1978; Kroger et al., 1980). Van Nevel and Demeyer (1977) found that as a consequence of shunting metabolic H_2 to propionate production via fumarate reductase less methane was produced than if CO_2 was reduced instead.

Ionophores may also exert a direct effect on other metabolic processes in rumen bacteria (Bergen and Bates, 1984). As a result of cation complexation and transport by monensin or lasalocid, the intracellular concentration of H^+

will increase thus decreasing the pH of the cell. A decline in the intracellular pH can effectively alter the oxidation-reduction potential of product forming reactions in the cell (Christensen and Cellarius, 1972). This would lead to a very rapid change in the fermentation pattern. Henderson et al. (1981) grew Ruminococcus albus in the presence of nonlethal monensin concentrations and reported a 200% increase in acetate production. An increase in H^+ within the cells stimulated the R. albus hydrogenase system to produce H_2 thus serving as an electron sink to regenerate NAD^+. The resultant decline in NADH allowed pyruvate to be metabolized to acetate rather than ethanol in this species (Bergan and Bates, 1984). Van Dyk and Veeger (1981) reported a similar affect of pH on the hydrogenase reaction in Megasphaera elsdenii. A similar phenomenon may be causing the immediate shift towards propionate production observed in the rumen when lasalocid or monensin are fed. The decreased intracellular pH may favorably influence the redox potentials of the components of the fumarate reductase electron transport chain in gram negative bacteria. NADH generated via NAD^+ reductase has been shown by Kroger (1977) to donate electrons to fumarate reductase in several ruminal strains. This coupled with higher total electromotive force from the low intracellular pH may drive the fumarate reductase reaction toward higher succinate yields and subsequently more propionate (Bergen and Bates, 1984). Enzymes themselves by virtue of their conformational

structure are pH sensitive and display maximum activity at a characteristic optimum pH (Lehninger, 1982). It is possible that the change in intracellular pH will allow increased activity of the enzyme systems involved in propionate synthesis.

The net effects of ionophores on rumen fermentation are: improved dietary energy values, a possible reduction in energy requirements of the animal, or both (Goodrich et al., 1984). The most consistent and well documented effect of ionophores is modification of volatile fatty acid (VFA) production in the rumen. The addition of either monensin or lasalocid to diets increases the molar proportion of propionate and reduces the molar proportions of acetate and butyrate (Richardson et al., 1976; Thornton et al, 1976; Brown and Davidovich, 1979; Chalupa, 1980; Thivend and Jouany, 1983; Ricke et al., 1984). Reduced methane production is often associated with the change in VFA proportions (Bartley et al., 1979; Fuller and Johnson, 1981; Thornton and Owens, 1981; Wedegaertner and Johnson, 1983). These changes improve the retention of carbon and energy in the rumen fermentation (Hungate, 1966; Chalupa, 1980) and thus would be expected to enhance animal performance. Richardson et al. (1976) estimated that 5.6% more gross energy is retained in the acid end products of fermentation when VFA ratios are changed from 60:30:10 (acetic, propionic and butyric) to 52:40:8 with monensin supplementation. Rowe et al (1981) fed sheep a 45% hay, 55% barley diet with and

without monensin at equal intakes and estimated VFA production by isotope dilution. Estimated VFA ratios were 84:6:10 (acetic, propionic and butyric) for control animals and 70:22:8 for monensin supplemented animals. In addition daily methane production was reduced by 39%. These authors calculated that monensin supplementation improved carbon retention in VFA by 18% and that this amounted to an 11% increase in gross energy retained in VFA. Owens (1980) summarized the data from numerous feedlot trials in which steers were fed high concentrate diets supplemented with monensin and lasalocid. In these trials the average effect of monensin was to reduce acetate 3.5 percentage units, increase propionate 5 percentage units, reduce butyrate 1.8 percentage units and reduce methane by 15% thus increasing fermentation efficiency 2.6%. The response to lasalocid was more variable with mean acetate decreases of 1.6 percentage units and propionate increases of 3.5 percentage units which would result in a 1.8% improvement in fermentation efficiency (Owens, 1980).

It has been suggested that the additional propionate may lower the heat increment (Blaxter and Wainman, 1964; Smith, 1979), spare glucogenic amino acids (Leng et al., 1967; Reilly and Ford, 1971) and stimulate body protein synthesis (Potter et al., 1968; Eskeland et al., 1974). However, the lower heat increment hypothesis has been disputed by Ørskov et al. (1979). In addition to the effects on ruminal VFA and methane production, ionophores

have been shown to increase the quantity of dietary protein escaping ruminal degradation. Poos et al. (1979) and Owens (1980) reported that monensin increased dietary protein bypass by 22 to 55% indicating a protein sparing effect.

Pressman (1976) has shown that carboxylic ionophores affect both the cell membrane and membranes of subcellular organelles of eukaryotic cells. Any membrane process or uptake system based on an electrical gradient, excitibility or osmoregulation may be modified by the ionophore if effective levels reach the tissue. Thus it is reasonable to assume that effects on host physiology may be involved in the production response seen when ionophores are fed to ruminants. The primary site of such effects would be the cell membranes of the mucosal cells in the small intestine (Donoho, 1984). Ionophores may also have an effect on rumen motility. Schelling (1984) has summarized the results of several grazing experiments utilizing cattle and concluded that monensin decreases rumen turnover rate and increases rumen fill.

In summary, carboxylic ionophores produce a large number of effects on rumen fermentation and animal physiology. All these effects appear to be caused by the basic mode of action of ionophores on transmembrane ion fluxes and dissipation of cation and proton gradients (Bergen and Bates, 1984).

D. BIBLIOGRAPHY

Ames, D.R. and D.R. Brink. 1977. Effect of temperature on lamb performance and protein efficiency ratio. J. Anim. Sci. 44:136.

Ames, D.R., D.R. Brink and R.R. Schalles. 1975. Relationship of ambient temperature and ADG. J. Anim. Sci. 41:262 (Abstr.).

Andu, A., I. Kusaka and S. Fukui. 1982. Na^+ dependent active transport systems for organic solutes in an alkalophilic Bacillus. J. Gen. Microbiol. 128:1057.

Baile, C.A. and J.M. Forbes. 1974. Control of feedintake and regulation of energy balance in ruminants. Physiol. Rev. 54:160.

Baile, C.A., C.L. McLaughlin, E.L. Potter and W. Chalupa. 1979. Feeding behavior changes of cattle during introduction of monensin with roughage of concentrate diets. J. Anim. Sci. 48:1501.

Bartley, E.E., E.L. Herod, R.M. Bechtle, D.A. Sapienze, B.E. Brent and A. Davidovich. 1979. Effect of monensin or lasalocid with or without niacin or amicloral, on rumen fermentation and feed efficiency. J. Anim. Sci. 49:1066.

Bergen, W.G. and D.B. Bates. 1984. Ionophores: Their effect on production efficiency and mode of action. J. Anim. Sci. 58:1465.

Berger, L.L., S.C. Ricke and G.C. Fahey, Jr. 1981. Comparison of two forms and two levels of lasalocid with monensin on feedlot cattle performance. J. Anim. Sci. 53:1440.

Blaxter, K.L. 1967. The Energy Metabolism of Ruminants. Hutchinson Scientific and Technical, London.

Blaxter, K.L. and F.W. Wainman. 1964. The utilization of the energy of different rations by sheep and cattle for maintenance and for fattening. J. Agr. Sci. (Camb.) 63:113.

Booth, I.R. and W.A. Hamilton. 1980. Energetics of bacterial amino acid transport. In: J.W. Payne (Ed.) Microorganisms and Nitrogen Sources. p 171. John Wiley and Sons Ltd., New York.

Brown, R.E. and A. Davidovich. 1979. The performance response to growing-finishing cattle fed graded levels of lasalocid. J. Anim. Sci. 49(Suppl. 1):358.

Burrin, D.G. and R.A. Britton. 1986. Response to monensin in cattle during subacute acidosis. J. Anim. Sci. 63:888.

Chai, K., P.M. Kennedy, L.P. Milligan and G.W. Mathison. 1985. Effects of cold exposure and plant species on forage intake, chewing behavior and digesta particle size in sheep. Can. J. Anim. Sci. 65:69.

Chalupa, W. 1980. Chemical control of rumen microbial metabolism. In: Y. Ruckebush and P. Thivend (Ed.) Digestive Physiology and Metabolism in Ruminants. p 325. AVI Publishing Co., Inc., Westport, CT.

Chen, M. and M.J. Wolin. 1979. Effect of monensin and lasalocid-sodium on the growth of methanogenic and rumen sacchrolytic bacteria. Appl. Environ. Microbiol. 38:72.

Cheng, K.J., R. Hironaka, G.A. Jones, T. Nicas and J.W. Costerton. 1976. Frothy feedlot bloat in cattle: Production of extracellular polysaccharides and development of viscosity in cultures of Streptococcus bovis. Can. J. Microbiol. 22:450.

Christensen, H.N. and R.A. Cellarius. 1972. Introduction to Bioenergetics: Thermodynamics for the Biologist. W.B. Saunders Co., Philadelphia. p 94.

Christopherson, R.J. 1976. Effects of prolonged cold and the outdoor winter environment on apparent digestibility in sheep and cattle. Can. J. Anim. Sci. 56:201.

Christopherson, R.J. 1985. Management and housing of animals in cold environments. In: M.K. Yousef (Ed.) Stress Physiology in Livestock, Vol. 1, Basic Principles. CRC Press, Boca Raton.

Christopherson, R.J. and P.M. Kennedy. 1983. Effect of the thermal environment on digestion in ruminants. Can. J. Anim. Sci. 63:477.

Christopherson, R.J. and J.R. Thompson. 1983. Can. J. Anim. Sci. 63:1019.

Christpoherson, R.J. and B.A. Young. 1986. Effects of cold environments on domestic animals. In: O. Gudmundsson (Ed.) Grazing Research in Northern Latitudes. pp. , Plenum Pub. Corp., New York.

Christopherson, R.J., J.R. Thompson, V.A. Hammond and G.A. Hills. 1978. Effects of thyroid status on plasma adrenaline and noradrenaline concentrations in sheep during acute and chronic cold exposure. Can. J. Physiol. Pharmacol. 59:490.

Colditz, P.J. and R.C. Kellaway. 1972. The effect of diet and heat stress on feed intake, growth and N-metabolism in Friesian, Brahman x Friesian and Brahman heifers. Aust. J. Agric. Res. 23:717.

De Voe, R.D. 1974. Principles of cell homeostasis. In: Medical Physiology (13th Ed.) p 3. C.V. Mosby Co., St. Louis, MO.

Dinnis, S.M., T.G. Nagaraja and E.E. Bartley. 1981a. Effects of lasalocid or monensin on lactate-producing or using rumen bacteria. J. Anim. Sci. 52:418.

Dinnis, S.M., T.G. Nagaraja and E.E. Bartley. 1981b. Effect of lasalocid or monensin on lactate production from in vitro fermentation of various carbohydrates. J. Dairy Sci. 64:2350.

Donoho, A.L. 1984. Biological studies on the fate of monensin in animals and in the environment. J. Anim. Sci. 58:1528.

Eddy, A.A. 1978. Energy coupling in microbial solute transport. In: F. Brommer and A. Kleinzeller (Ed.) Current Topics in Membranes and Transport, Vol 10. p 35. Academic Press, New York.

Elam, C.J. 1970. Problems related to intensive indoor and outdoor beef production systems. J. Anim. Sci. 32:554.

Eskeland, B., W.H. Pfander and R.L. Preston. 1974. Intravenous energy infusion in lambs: Effects on nitrogen retention, plasma free amino acids and plasma urea nitrogen. Brit. J. Nutr. 31:201.

Fitzgerald, P.R. 1975. The significance of bovine coccidiosis as a disease in the United States. Bovine Pract. 10:28.

Fitzgerald, P.R. and M.E. Mansfield. 1973. Efficacy of monensin against bovine coccidiosis in young Holstein - Friesian calves. J. Protozool. 20:121.

Freer, M., R.C. Campling and C.C. Balch. 1962. Factors affecting the voluntary intake of food by cows. 4. The behaviour and reticular motility of cows receiving diets of hay, oat straw and oat straw with urea. Br. J. Nutr. 16:279.

Fregly, M.J., F.P. Field, M.J. Katovich and C.C. Barney. 1979. Fed. Proc. 38:2162.

Fuller J.R. and D.E. Johnson. 1981. Monensin and lasalocid effects on fermentation in vitro. J. Anim. Sci. 53.1574.

Garrett, W.N. and D.E. Johnson. 1983. Nutritional energetics of ruminants. J. Anim. Sci. 57(Suppl. 2):478.

Gonyou, H.W., R.J. Christopherson and B.A. Young. 1979. Effects of cold temperature and winter conditions on some aspects of behavior of feedlot cattle. Appl. Anim. Ethol. 5:113.

Goodrich, R.D., J.E. Garrett, D.R. Gast, M.A. Kirick, D.A. Larson and J.C. Meiske. 1984. Influence of monensin on the performance of cattle. J. Anim. Sci. 58:1484.

Gordon, E.E. and M. de Hartog. 1968. Valinomycin-stimulated glycolysis in Ehrlich ascites tumor cells. Biochim. Biophys. Acta 162:220.

Graham, A.D. and R.J. Christopherson. 1981. Effects of adrenaline and noradrenaline on the heat production of warm and cold acclimated sheep. Can. J. Physiol. Pharmacol. 59:985.

Gregg, V.A. and L.P. Milligan. 1982. Role of Na^+, K^+-ATPase in muscular energy expenditure of warm- and cold-exposed sheep. Can. J. Anim. Sci. 62:123.

Haynes, D.H. and B.C. Pressman. 1974. X537 A: A Ca^{2+} ionophore with a polarity-dependent and complexation-dependent fluorescence signal. J. Membrane Biol. 16:195.

Haynes, D.H., V.C. Chiu and B Watson. 1980. Study of the Ca^{2+} transport mechanism of X527 A in phospholipid membranes using fluoresence and rapid kinetic techniques. Arch. Biochem. Biophys. 203:73.

Henderson, C., C.S. Stewart and F.V. Nakrep. 1981. The effect of monensin on pure and mixed cultures of rumen bacteria. J. Appl. Bacteriol. 51:159.

Herald, F. and F.W. Knapp. 1980. Effects of monensin on development of the face fly and the horn fly. J. Econ. Entomol. 73:762.

Herald, F., F.W. Knapp, S. Brown and N.W. Bradley. 1982. Efficacy of monensin as a cattle feed additive against the face fly and horn fly J. Anim. Sci. 54:1128.

Hidiroglou, M. and J.R. Lessard. 1971. Some effects of fluctuating low ambient temperatures on beef cattle. Can. J. Anim. Sci. 51:111.

Hobson P.N. and R. Summers. 1967. The continous culture of anaerobic bacteria. J. Gen. Microbiol. 47:53.

Hobson, P.N. and R. Summers. 1972. ATP pool and growth in Selanomonas ruminantium. J. Gen. Microbiol. 70:351.

Hoffman, M.P. and H.L. Self. 1970. Shelter and feedlot surface effects on performance of yearling steers. J. Anim. Sci. 31:967.

Hungate, R.E. 1966. The Rumen and its Microbes. Academic Press, New York. p 282.

Ingalls, J.R. and M.E. Seale. 1967. Dairy bulls and steers in open vs. heated housing. J. Anim. Sci. 26:1467.

Johnson D.E. and J.C. Crownover. 1975. Energy requirements of feedlot cattle in north central Colorado: Variation in maintenance requirements by month. Research Highlights of the Animal Sciences Department. General Series 948. Colorado State Univ. Fort Collins. pp. 46.

Jolliffe, L.K., R.J. Doyle and U.N. Strips. 1981. The energetic membrane and energized cellular autolysis in Bacillus subtilis. Cell 25:753.

Kennedy, P.M. 1985. Influences of cold exposure on digestion of organic matter, rates of passage of digesta in the gastrointestional tract, and feeding and rumination behavior in sheep given four forage diets in the chopped, or ground and pelleted form. Br. J. Nutr. 53:159.

Kennedy, P.M. and L.P. Milligan. 1978. Effects of cold exposure on digestion, microbial synthesis and nitrogen transformation in sheep. Br. J. Nutr. 39:105.

Kennedy, P.M., R.J. Christopherson and L.P. Milligan. 1976. The effect of cold exposure of sheep on digestion, rumen retention time and efficiency of microbial synthesis. Br. J. Nutr. 36:231.

Kennedy, P.M., R.J. Christopherson and L.P. Milligan. 1982. Effect of cold exposure on feed protein degradation, microbial protein synthesis and transfer of plasma urea to the rumen of sheep. Br. J. Nutr. 47:521.

Kennedy, P.M., R.J. Christopherson and L.P. Milligan. 1986. Digestive responses to cold. In: L.P. Milligan, W.L. Grovum and A. Dobson (Eds.) Control of Digestion and Metabolism in Ruminants. pp. 285-306. Reston Publishing Co., Reston.

Kitada, M. and K. Horikoshi. 1982. Energy coupling reactions of the active transport system for *a*-aminobutyric acid in alkalophilic Bacillus no. 8-1. Agr. Biol. Chem. 46:1115.

Knox, K.L. and T.M. Handley. 1973. The California net energy system. Theory and Application. J. Anim. Sci. 37:190.

Kroger, A. 1977. Phosphorylative electron transport with fumarate and nitrate as terminal hydrogen acceptors. In: B.A. Haddock and W.A. Hamilton (Ed.) Microbial Energetics. p 61. Cambridge Univ Press, Cambridge.

Kroger, A., E. Dorrer and E. Winkler. 1980. The orientation of the substrate sites of formate dehydrogenase and fumarate reductase in the membrane of Vibrio succinogenes. Biochim. Biophys. Acta 589:118.

Lehninger, A.L. 1982. Principles of Biochemistry. Worth Publishers, New York. p 218.

Lemenager, R.P., F.N. Owens, B.J. Shockey, K.S. Lusby and R. Totusek. 1978. Monensin effects on rumen turnover rate, twenty - four hour VFA pattern, nitrogen components and cellulose disappeatance. J. Anim. Sci. 47:255.

Leng, R.A., J.W. Steele and J.R. Luick. 1967. Contribution of propionate to glucose synthesis in sheep. Biochem. J. 103:785.

Leu, B.M., M.P. Hoffman and H.L. Self. 1977. Comparison of confinement, shelter and no shelter for finishing yearling steers. J. Anim. Sci. 56:717.

Levinson, C. 1967. Effect of valinomycin on net sodium and potassium transport in Ehrlich ascites tumor cells. Nature 216:74.

McBride, G.E. and R.J. Christopherson. 1984. Effects of cold exposure on young growing lambs. Can. J. Anim. Sci. 64:379.

McDougald, L.R. 1978. Monensin for the prevention of coccidiosis in calves. Amer. J. Vet. Res. 39:1748.

Mertens, D.R. 1977. Dietary fiber components: relationship to the rate and extent of ruminal digestion. Fed. Proc. 36:187.

Milligan, J.D. and G.I. Christison. 1974. Effects of severe winter conditions on performance of feedlot steers. Can. J. Anim. Sci. 54:605.

Mitchell, P. 1961. Coupling of phosphorylation to electron and hydrogen transfer by a chemiosmotic type of mechanism. Nature 191:144.

Monteith, J.L. and L.E. Mount. 1974. Heat Loss from Animals and Man. Butterworths, London.

Morris, L. 1961. Photoperiodicity of seasonal rythm of wool growth in sheep. Nature (London). 190:102.

Muhamad, Y.B., M.P. Hoffman and H.L. Self. 1983. Influence of different ratios of corn and corn silage, housing systems and seasons on the performance of feedlot steers. J. Anim. Sci. 56:747.

NRC. 1984. Nutrient Requirements of Domestic Animals, No. 4. Nutrient Requirements of Beef Cattle. Sixth Revised Ed. National Academy of Sciences-National Research Council, Washington, DC.

Nagaraja, T.G., T.B. Avery, E.E. Bartley, S.J. Galitzer and A.D. Dayton. 1981. Prevention of lactic acid acidosis in cattle by lasalocid or monensin. J. Anim. Sci. 53:206.

Nagaraja, T.G., T.B. Avery, E.E. Bartley, S.K. Roof and A.D. Dayton. 1982. Effect of lasalocid, monensin or thiopeptin on lactic acidosis in cattle. J. Anim. Sci. 54.649.

Nicholson, J.W.G., R.E. McQueen and P.L. Burgess. 1980. Effect of cold on digestibility of chopped or pelleted hay by sheep. Can. J. Anim.Sci. 60:571 (Abstr.).

Ørskov, E.R., D.A. Grubb, J.S. Smith, A.J.F. Webster and W. Corrigall. 1979. Efficiency of utilization of volatile fatty acids for maintenance and energy retention by sheep. Brit. J. Nutr. 41:541.

Ovchinnikov, Y.A., V.T. Ivanov and A.M. Shkrob. 1974. Membrane-Active Complexones. Elsevier Scientific Pub. Co., Amsterdam. p 343.

Owens, F.N. 1980. Ionophore effects on utilization and metabolism of nutrients - Ruminants. Proc. Georgia Nutr. Conf., Univ. of Georgia, Athens, p. 17.

Painter, G.R., R. Pollack and B.C. Pressman. 1982. Conformational dynamics of the carboxylic ionophore lasalocid A underlying cation complexation - decomplexation and membrane transport. Biochemistry 21:5613.

Poos, M.I., T.L. Hanson and T.J. Klopfenstein. 1979. Monensin effects on diet digestibility, ruminal protein bypass and microbial protein synthesis. J. Anim. Sci. 48:1516.

Potter, E.L., D.B. Purser and J.H. Cline. 1968. Effects of various energy sources upon plasma free amino acids in sheep. J. Nutr. 95:665.

Potter, E.L., C.O. Cooley, L.F. Richardson, A.P. Raun and R.P. Rathmacher. 1976. Effect of monensin on performance of cattle fed forage. J. Anim. Sci. 43:665.

Pressman, B.C. 1976. Biological application of ionophores. Ann. Rev. Biochem. 45:501.

Reddy, C.A. and H.D. Peck, Jr. 1978. Electron transport phosphorylation coupled to fumarate reduction by H_2 and Mg^{++}-dependent adenosine triphosphatase activity in extracts of the rumen anaerobic Vibrio succinogenes. J. Bacteriol. 134:982.

Reilly, P.E.B. and E.J.H. Ford. 1971. The effects of dietary contents of protein on amino acid and glucose production and the contribution of amino acids to gluconeogenesis in sheep. Brit. J. Nutr. 26:24.

Richardson, L.F., A.P. Raun, E.L. Potter, C.O. Cooley and R.P. Rathmacher. 1976. Effect of monensin on rumen fermentation in vitro and in vivo. J. Anim. Sci. 43:657.

Ricke, S.C., L.L. Berger, P.J. van der Aar and G.C. Fahey, Jr. 1984. Effect of lasalocid and monensin on nutrient digestion, metabolism and rumen characteristics of sheep. J. Anim. Sci. 58:194.

Robertshaw, D. 1985. Heat loss of cattle. In: M.K. Yousef (Ed.) Stress Physiology in Livestock, Vol. 1, Basic Principles. CRC Press, Boca Raton.

Rosen, B.P. and E.R. Kashket. 1978. Energetics of active transport. In: B.P. Rosen (Ed.) Bacterial Transport. p 560. Marcel Dekker Inc., New York.

Rowe, J.B., A. Davis and A.W.J. Broome. 1981. Quantative changes in the rumen fermentation of sheep associated with feeding monensin. Proc. Nutr. Soc. 41:3A.

Sakauchi, R. and S. Hoshino. 1981. Effects of monensin on ruminal fluid viscosity, pH, volatile fatty acids and ammonia levels, and microbial activity and population in healthy and bloated feedlot steers. Tierphysiol. Tierernahrt. und Futtermittelnde 46:21.

Sandeaux, R., J. Sandeaux, J.C. Govach and B. Brun. 1982. Transport of Na^+ by monensin across bimolecular lipid membranes. Biochim. Biophys. Acta 684:127.

Sasaki, Y. and T.E.C. Weekes. 1986. Metabolic responses to cold. In: Milligan, L.P., W.L. Grovum and A. Dobson (Eds.) Control of Digestion and Metabolism in Ruminants. pp. 326-343. Reston Publishing Co., Reston.

Schelling, G.T. 1984. Monensin mode of action in the rumen. J. Anim. Sci. 58:1518.

Slee, J. 1985. Physiological responses and adaptations of sheep. In: M.K. Yousef (Ed.) Stress Physiology in Livestock. pp. 111. CRC Press, Inc., Boca Raton.

Smith, G.E. 1979. Energy metabolism and metabolism of the volatile fatty acids. In: D.C. Church (Ed.) Digestive Physiology and Nutrition of the Ruminant. p 629. Oregon State Univ. Bookstore, Inc., Corvallis.

Spears, J.W. and R.W. Harvey. 1984. Performance, ruminal and serum characteristics of steers fed lasalocid on pasture. J. Anim. Sci. 58:460.

Stockdale, P.H.G. and W.D.G. Yates. 1978. Resistance to **Eimeria zuernii** produced after chemotherapy of experimental infection in calves. Vet. Parasitol. 4:209.

Thauer, R.K., K. Jungermann and K Decker. 1977. Energy conservation in chemotrophic anaerobic bacteria. Bacteriol. Rev. 41:100.

Thivend, P. and J.P. Jouany. 1983. Effect of lasalocid sodium on rumen fermentation and digestion in sheep. Reprod. Nutr. Develop. 23:817.

Thonney, M.K., E.K. Heide, D.J. Duhaime, R.J. Hand and D.J. Perosis. 1981. Growth, feed efficiercy and metabolite concentrations of cattle fed high forage diets with lasalocid or monensin supplements. J. Anim. Sci. 52:427.

Thornton, J.H., F.N. Owens, R.P. Lemenager and R. Totusek. 1976. Monensin and ruminal methane production. J. Anim. Sci. 43:336.

Thornton ,J.H. and F.N. Owens. 1981. Monensin supplementation and in vivo methane production by steers. J. Anim. Sci. 52:628.

Van Dyk, C. and C. Veeger. 1981. The effects of pH and redox potential on the hydrogen production activity of the hydrogenase from Megasphaera elsdenii. Eur. J. Biochem. 114:209.

Van Es, A.J.H. and Y. van der Honing. 1979. Energy utilization. In: W.H. Broster and H. Swan (Eds.). Feeding Strategy for the High Yielding Dairy Cow. pp. 68. Granada Publishing, London.

Van Nevel, C.J. and D.I. Demeyer. 1977. Effect of monensin on rumen metabolism in vitro. Appl. Environ. Microbiol. 34:251.

Wallace, R.J., J.W. Czerkawski and G. Breckenridge. 1981. Effect of monensin on the fermentation of basal rations in the rumen simulation technique. (rusitec). Brit. J. Nutr. 46:131.

Warren, W.P., F.A. Martz, H.K. Asay, E.S. Hilderbrand, C.G. Payne and J.R. Vogt. 1974. Digestibility and rate of passage by steers fed tall fescue, alfalfa and orchard grass hay in 18 and 32 C ambient temperatures. J. Anim. Sci. 39:93.

Webster, A.J.F. 1970. Direct effects of cold weather on the energetic efficiency of beef production in different regions of Canada. Can. J. Anim. Sci. 50:563.

Webster, A.J.F. 1971. Prediction of heat losses from cattle exposed to cold outdoor environments. J. Appl. Physiol. 30:684.

Webster, A.J.F. 1974. Physiological effects of cold exposure. In: D. Robertshaw (Ed.) Environmental Physiology p 33. Butterworths, London.

Webster, A.J.F. 1976. Effects of cold on endocrine responses of ruminants and other domestic animals. In: H.D. Johnson (Ed.) Progress in Biometeorology. B. Progress in Animal Biometeorology. Vol. 1. pp 33. Swets and Zeilinger. B.V., Amsterdam.

Webster, A.J.F. 1978. Prediction of the energy requirements for growth in beef cattle. Wld. Rev. Nutr. Diet. 30:189.

Webster, A.J.F., A.M. Hicks and F.L. Hays. 1969. Cold climate and cold temperature induced changes in the heat production and thermal insulation of sheep. Can. J. Physiol. Pharmacol. 44:553.

Webster, A.J.F., J. Chlumecky and B.A. Young. 1970. Effects of cold environments on the energy exchanges of young beef cattle. Can. J. Anim. Sci. 50:80.

Wedegaertner, T.C. and D.E. Johnson. 1983. Monensin effects on digestibility, methanogenesis and heat increment of a cracked corn-silage diet fed to steers. J. Anim. Sci. 57:168.

Weston, R.H. 1983. Proc. Nutr. Soc. Aust. 8:181.

Westra, R. and R.J. Christopherson. 1976. Effects of cold on digestibility retention time of digesta, reticulum motility and thyroid hormones in sheep. Can. J. Anim. Sci. 56:699.

Wilson, D.B. and J.B. Smith. 1978. Bacterial transport proteins. In: B.P. Rosen (Ed.) Bacterial Transport. p 495. Marcel Deckker Inc., New York.

Young, B.A. 1975a. Temperature induced changes in metabolism and body weight of cattle (*Bos taurus*). Can. J. Physiol. Pharmacol. 53:947.

Young, B.A. 1975b. Effects of winter acclimatization on resting metabolism of beef cows. Can. J. Anim. Sci. 55:619.

Young, B.A. 1981. Cold stress as it affects animal production. J. Anim. Sci. 52:154.

Young, B.A. 1983. Ruminant cold stress: effect on production. J. Anim. Sci. 57:1601.

Young, B.A. 1985. Physiological responses and adaptation of cattle. In: M.K. Yousef (Ed.) Stress Physiology in Livestock (Vol. 1). pp. 102-108. CRC Press, Inc., Boca Raton.

Young, B.A. and A.A. Degan. 1981. Thermal influences on ruminants. In: J.H. Clark (Ed.) Environmental Aspects of Housing for Animal Production. p. 167. Butterworths, London.

Yousef, M.K. 1985. Thermoneutral zone. In: M.K. Yousef (Ed.) Stress Physiology in Livestock, Vol. 1, Basic Principles. CRC Press, Boca Raton.

III. EFFECT OF LASALOCID ON FEEDLOT PERFORMANCE AND ENERGETIC EFFICIENCY OF CATTLE.

A. INTRODUCTION

Lasalocid is a carboxylic ionophore which has been used as a feed additive for ruminants. In numerous feeding trials, lasalocid has improved feed efficiency and rate of gain in ruminants fed high concentrate diets (Brethour, 1979; Brown and Davidovich, 1979; Kuhl et al., 1980; Berger et al., 1981b). Lasalocid is also effective when added to high roughage diets resulting in decreased feed to gain ratios and increased growth rates (Thonney et al., 1981; Guiterrez et al., 1982; Spears and Harvey, 1984). The means by which this improvement in animal performance is achieved is not fully understood but it is believed that several factors are involved (Schelling, 1984).

Lasalocid was first isolated, purified and shown to have antimicrobial activity by Berger et al. (1951). The biological properties of lasalocid include an ability to greatly influence the movement of a range of mono- and divalent cations as well as biogenic amines (e.g. epinephrine and norepinephrine) across membranes. Pressman (1973, 1976) has thoroughly reviewed the properties and applications of lasalocid. The mode of action of lasalocid is to induce a non-physiological ion leak across cell membranes which causes a dissociation of metabolism from useful cellular functions (Bergen and Bates, 1984). Cells

with the capacity to produce at least some ATP by electron transport will survive and continue to grow when exposed to lasalocid, but at a higher maintenance cost. Cells which must generate their ATP by substrate level phosphorylation cannot meet this demand and lyse. The net effect is that gram positive bacteria tend to be inhibited by lasalocid while gram negative rumen bacteria survive (Chen and Wolen, 1979; Dinnis et al., 1981). Changes in microbial populations then, may be a factor involved in the improvement in feed efficiency of cattle fed ionophores.

The most consistent and well documented effect of ionophores is modification of volatile fatty acid (VFA) production in the rumen. The addition of lasalocid to diets increases the molar proportion of propionate and reduces the molar proportions of acetate and butyrate (Bartley et al., 1979; Brown and Davidovich, 1979; Fuller and Johnson, 1981; Thivend and Jouany, 1983; Ricke et al., 1984; Spears and Harvey, 1984). It has been suggested that increases in propionate production in the rumen relative to acetate may result in improvements in the efficiency of energy utilization through a lowering of the heat increment of feeding. However there is also considerable evidence that alterations in the ratio of acetate to propionate within the limits reported for lasalocid supplemented diets do not substantially influence the efficiency of energy utilization for growth (Bull et al., 1970; Johnson, 1972; Johnson et al., 1974; Orskov et al., 1979). Increased propionate

availability may also spare amino acids normally used for gluconeogenesis and stimulate protein synthesis (ARC, 1980; Bergen and Bates, 1984).

A reduction in methane production is tied to the shift in rumen microbial population which occurs in response to lasalocid. In vitro studies of rumen fermentation demonstrated a marked reduction in methane synthesis when lasalocid was added to the fermentation substrate (Bartley et al., 1979; Fuller and Johnson, 1981). Reduced methane losses partially explain the increase in metabolizability of dietary energy which is observed when an ionophore is added to ruminant diets (Thornton and Owens, 1981; Wedegaertner and Johnson, 1983).

Ionophores have been shown to decrease the rate of passage of ingesta through the digestive tract of ruminants (Schelling, 1984). This changes both the extent and the site of digestion of dietary organic matter within the gastrointestinal tract (Bartley et al., 1979; Paterson et al., 1983; Thivend and Jouany, 1983; Ricke et al., 1984). Although studies with high concentrate, low fiber diets supplemented with lasalocid are lacking, Muntifering et al. (1981) have examined the effects of monensin (a similar carboxylic ionophore) at 33 $mg \cdot kg^{-1}$ diet in a diet containing 90% whole shelled corn. Monensin supplementation resulted in a slight depression in ruminal digestion of starch and crude protein coupled with an increase in digestion of these components within the animal. This

implies that a greater proportion of the feed nitrogen and starch were digested post-ruminally with possible greater efficiency of utilization of the end products of digestion.

Some researchers believe that the contribution of the above factors in improving digestive efficiency only explains a portion of the feed efficiency response achieved with ionophores. It has been postulated that the chemicals also elicit some kind of other beneficial response within the animal (Bergen and Bates, 1984; Schelling, 1984). Garrett (1982) has suggested that there is a decrease in fasting heat production (HeE) and the animal's energy requirements for maintenance when an ionophore is fed. Byers' (1980) work suggests that there was an increase in the net energy for maintenance (NEm) value of the diet or a decreased maintenance requirement when ionophores are supplemented. It is known that feeding ionophores can increase glucose turnover rates (Van Maanan et al., 1978) and decrease amino acid utilization for gluconeogenesis (Beede et al., 1980). Such metabolic changes within the animal suggest that endocrine changes may also be occuring which may affect energy partitioning within the animal.

The objectives of these experiments were to quantify the effects of supplemental lasalocid on the performance and feed efficiency of cattle fed a high concentrate, barley-based diet and to determine the mechanisms by which these responses were mediated.

B. MATERIALS AND METHODS

Experiment 1

One hundred heifers of predominantly Hereford breeding were purchased from a local commission firm for this experiment. Upon arrival the heifers were ear-tagged; given a 2 ml intramuscular injection containing 1000000, 300000 and 100 IU of vitamins A, D and E respectively; and vaccinated with Coopavax-8[1] vaccine as well as with Infectious Bovine Rhinotracheitus[2] vaccine. The heifers were treated with Tramisol obletes[3] for worm control. No growth promotant implants were used. The animals were fed cereal and grass silage and hay during the 25 d adjustment period. On the third last day of the adjustment period 2 kg barley·head^{-1}·d^{-1} was included in the ration.

The heifers were ranked according to liveweight and separated into two groups; one heavy (327 kg initial weight) and one light (290 kg initial weight). Each group of heifers was allotted to an open-front shed which partially covered ten identical pens (4x8 m), yielding one shed containing light heifers and one shed containing heavy heifers. Within each shed the pen weights were approximately equal. Five dietary treatments (lasalocid at 0, 24, 36 and 54 mg·kg^{-1} dry matter (DM) and monensin at 33

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[1]Cooper Products Division, Burroughs Wellcome Ltd., La Salle, Quebec.
[2]Dekkon Laboratories Inc., Division of Biologies Corp., Omaha, NE.
[3]Cyanamid Canada Inc., Montreal, Quebec.

$mg \cdot kg^{-1}$ DM) were imposed on the heifers such that there were five animals per pen and two pens per treatment within each shed. At the begining of the 98 day experimental feeding period a ration containing 45% concentrate and 55% chopped alfalfa-grass hay was offered. The concentrate portion of the diet was increased by 15 percentage units every five days. Thus by day 15 the final diet consisting of 90% concentrate and 10% roughage was being fed. The amount of lasalocid[4] added to the concentrate portion of the diet was varied in this initial 15 day period to ensure that there was a uniform concentration of drug (0, 24, 36 and 54 $mg \cdot kg^{-1}$ dietary dry matter (DM)) in the total diet throughout the feeding period (table III.1). For the monensin treatment group, monensin was added to the concentrate to provide a level of 11 $mg \cdot kg^{-1}$ dietary DM in the first 28 days and 33 $mg \cdot kg^{-1}$ dietary DM for the remainder of the experiment. The composition of the diets is given in table III.2. All pens were fed ad libitum with no additional salt or minerals offered free choice.

Initial and final weights were averages of weights taken on three consecutive days. Heifers were weighed every 2 wk throughout the feeding period. Feed was removed and water withheld approximately 16 h before weights were taken.

The heifers received their experimental diet at a slightly reduced feeding level for 3 d after the last weigh day, and then were slaughtered at a local abbatoir.

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[4]Hoffmann-La Roche Ltd., Etobicoke, Ontario.

Dressing percentages were calculated on the basis of hot carcass weights and the final feedlot weight. Carcasses were graded and rib eye area and back fat depth (average at top, middle and bottom of the rib eye between the 11th and 12th rib) measured by Agriculture Canada personnel (Anonymous, 1978).

Samples of hay and each concentrate mixture were obtained at various times during the 98 d experiment. Individual samples were analysed for DM by drying at 110 C in a forced-air oven to a constant weight, and for crude protein, calcium and phosphorus by standard methods (AOAC, 1980).

Carcass data on individual animals were analysed by two-way analysis of variance (Steel and Torrie, 1980). Pen means for DM intake, weight gain and DM per gain were analysed similarly. Where appropriate, treatment means were compared by Student-Newman-Keuls' test (Steel and Torrie, 1980).

Experiment 2

Four mature steers (616 kg) of mixed breeding (predominantly Hereford and Angus plus varying amounts of Galloway, Limousin and Charolais), which had previously been adapted to metabolism crates and a confinement-type respiration chamber, were used to measure the effect of lasalocid on diet digestibility, metabolizability and energy partitioning. The steers were fed the same basal diet as

used in experiment 1 with either 0 or 36 mg·kg^{-1}DM of lasalocid added (table III.1).

Measurements were made at four feeding levels (21, 44, 67 and 89 g DM·kg$^{-.75}$, estimated to be 0.5, 1.0, 1.5 and 2.0 times maintenance) during each half of the experiment. At the begining of the first half of the experiment two steers were assigned to the diet containing 36 mg lasalocid·kg^{-1} DM and the other two were assigned to the diet with no lasalocid. One animal on the lasalocid supplemented diet was fed at the highest feeding level and the other at the lowest feeding level. The same procedure was followed for the diet with no lasalocid. The feeding level was then adjusted in a stepwise fashion between each measurement for each steer. For the second half of the experiment, the two steers which received the lasalocid supplemented diet were switched to the diet without lasalocid and the two steers which were fed the diet without lasalocid were switched to the diet containing lasalocid. Within each dietary treatment, steers were assigned to feeding levels in the same manner as in the first half of the experiment. Thus at the end of the experiment each steer had received both the diets with and without lasalocid at each of the four feeding levels.

Diets were fed at the assigned feeding level for a 14 d adaptation period. This was followed by a 7 d period during which a total collection of feces and urine was made, and then by a 24 h period in which calorimetric measurements

were made. Steers were fed twice daily throughout the experiment except when fasting heat production (HeE) measurements were taken during the 72-96 h period after the animals had been fed at the 44 g DM·kg$^{-.75}$ (approximately maintenance) feeding level.

Two days prior to the heat production measurements, animals were fitted with a jugular vein catheter for blood sampling. In the second half of the experiment rumen fluid samples were taken at this time as well (8 h after feeding). Blood samples were collected after the catheter had been inserted for 18 h. Three 10 ml blood samples were taken from each animal every 2 h for 10 h, with the first sample being taken just before the morning feeding. Blood was collected into plain tubes without anticoagulant and placed on ice for insulin and growth hormone assays. Serum was separated from the cells by centrifugation as soon as possible after collection, usually within 20 min, and stored frozen at -20 C in tightly sealed vials until analyses. Blood for glucagon assays was collected in glass tubes containing 14 mg Na-EDTA (anticoagulant) and 1 mg aprotinin (proteolytic enzyme inhibitor), immediately placed on ice and then centrifuged. Plasma was stored at -20 C until analysis.

Respired gasses were measured with an open-circuit calorimetery system attached to an animal chamber. The system was similar to that previously described by Young et al. (1975). The animal chamber described by Young et

al. (1975) was also altered slightly to permit open-circuit operation by addition of a line to the chamber to supply outside air. Air was drawn through the animal chamber and the gas metering system at a constant rate by two rotery vane pumps (Gast model 1022-V103)[5]. The air flow rate was measured using a rotameter (Fischer and Porter series 99A001U64)[6] which was calibrated to have a full scale flow at standard temperature and pressure of 727.3 liters per minute. Temperature and humidity of the air from the animal chamber was measured with a wet and dry bulb thermocouple arrangement (Bailey model BAT-8C)[7]. Samples of air from the animal chamber were continuously drawn off, after the air exited from the rotameter, by a small pump. The sampled air was passed through a $CaSO_4$ drying tube and then through a manifold from which it was delivered to each of the analyzers. Oxygen concentration of the air was determined using a Beckman paramagnetic analyzer[8] (model F3M). Beckman infrared analyzers were used for carbon dioxide (model 864) and methane (model 215A) determination. The analyzers were calibrated and checked every few hours against gas mixtures of known composition. Outside air was one mixture. The other was a prepared mixture of oxygen, carbon dioxide, methane and nitrogen. The total volume of air which passed through the chamber during a 24 h measurement period was corrected to standard temperature and pressure. Liters of

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[5]Gast Manufacturing Corp., Benton Harbor MI.
[6]Fischer and Porter Co., Warminster PA.
[7]Bailey Instruments, Saddle Brook NJ.
[8]Beckman Instruments Inc., Fullerton CA.

oxygen consumed and carbon dioxide and methane produced were computed from the difference in composition of the air exausted from the chamber and the outside air times the corrected total volume of air which passed through the system during the measurement period. Heat production (HE) was then calculated as HE ($kcal \cdot d^{-1}$) = 3.866 x O_2 ($l \cdot d^{-1}$) + 1.200 x CO_2 ($l \cdot d^{-1}$) - 0.518 x CH_4 ($l \cdot d^{-1}$) - 1.431 x urine-N ($g \cdot d^{-1}$) (Brouwer, 1965).

Hay and concentrate were weighed separately for each steer and presacked in advance for each adaptation, collection and gas measurement period. Samples of each feedstuff were taken during this meal preparation and stored at -20 C until analysed.

An aliquot of daily fecal output was collected and stored at -20 C. At the end of each 7 d collection period the feces samples were dried at 60 C, ground and pooled to yield individual animal composites, which were stored at -20 C for later analysis. Daily urine output was collected over 100 ml 5N HCl containing 1 $g \cdot l^{-1}$ mercuric chloride. Daily aliquots of urine were pooled on the day collected and the composite sample for each animal was stored at -20 C.

Rumen fluid samples were strained through two layers of cheesecloth and a 5 ml aliquot was obtained. One ml of 25% metaphosphoric acid and 1 ml of caproic acid (3.6 $mg \cdot ml^{-1}$, internal standard) were added. The sample was thoroughly mixed, centrifuged and the clear supernatent stored at -20 C.

Dry matter of the feed and feces was determined by oven drying at 110 C to a constant weight. Nitrogen in the feed, feces and urine was determined by standard macro-Kjeldahl procedure (AOAC, 1980). Gross energy content of the feed, feces and urine were determined in an automatically controlled Parr adiabatic bomb calorimeter[9]. Volatile fatty acid (VFA) concentrations were determined on a Bendix model 2526-1 gas chromatograph[10] with a flame ionization detector. The glass column was 1.22 m long, 3 mm in diameter, and packed with 80/100 mesh Chromosorb 101[11]. Column temperature was varied from 150 C to 190 C at 5 C·min^{-1}.

Prior to determining hormone levels, serum or plasma samples for each hormone were pooled within animal and feeding level and the resulting composite sample used for analysis. For each hormone, all samples were assayed in duplicate in one assay. Insulin levels were measured by a solid phase radioimmunoassay (RIA) procedure[12]. Intraassay coefficient of variation (CV) for the insulin procedure was 5.8%. Concentrations of glucagon were determined using a double antibody technique[13]. The intraassay CV for the glucagon RIA was 9.6%. Growth hormone levels were analysed using ^{125}I-growth hormone prepared using a modification of the procedure of Greenwood et al. (1963) and utilizing a

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[9]Parr Instrument Co., Moline, Il.
[10]Bendix Corp., Process Instrument Division, Roncerverte, WV.
[11]Sigma Chemical Co., St. Louis, MO.
[12]Coat-A-Count, Diagnostic Products Corp., Los Angeles, CA.
[13]^{125}I-glucagon RIA kit, Cambridge Medical Diagnostics Inc., Billerica, MA.

double antibody RIA (Laarveld et al., 1986). Intraassay CV was 8% with this procedure.

The data were analysed as a split-plot design using least-squares analysis of variance (Steel and Torrie, 1980). Feeding levels were tested against the period within feeding level term. The treatment and treatment by level interaction were tested against the error term. Feeding level means were tested for linear and quadratic effects by orthogonal comparisons.

C. RESULTS

Experiment 1

Initial and final weights, average daily gain, DM consumption and DM·kg^{-1} gain of heifers fed the five diets are presented in table III.3. Addition of monensin or lasalocid to the basal diet did not affect feed consumption at any time during the feeding period. Significant differences in growth rate ($P<.05$) were only apparent during the first 28 days of the trial at which time heifers fed the highest level of lasalocid gained the fastest. In subsequent feeding periods there were no differences in gain between treatment groups. Heifers fed the diets supplemented with lasalocid or monensin tended to grow faster ($P=.12$) than control heifers (9.7 and 4%, respectively). Heifers in the heavy weight group grew faster ($P<.05$) than heifers in the lighter weight group

(1.36 vs 1.29 $kg \cdot d^{-1}$) however there was no effect ($P>.1$) of initial weight of the animals on their response to dietary treatment.

Heifers fed 54 $mg \cdot kg^{-1}$ lasalocid or monensin required less ($P<.05$) $DM \cdot kg^{-1}$ gain than did the control animals in the first 28 d period. Heifers fed diets containing lasalocid at 36 or 54 $mg \cdot kg^{-1}$ tended to have better feed efficiency than control animals ($P<.1$).

Dietary treatment had no influence ($P>.1$) on carcass characteristics or the incidence of abcessed livers (table III.3).

Experiment 2

Dry matter intake and nutrient digestibilities are presented in table III.4. Increasing feeding level from 21 to 89 g $DM \cdot kg^{-.75}$ resulted in a significant ($P<.05$) increase in the digestibility of DM and energy for steers fed the control diet. The greatest increase appeared between the lowest two feeding levels; over this interval digestibilities of DM and energy improved approximately 10 digestibility units. A similar trend was seen for steers fed the lasalocid supplemented diet. However with the lasalocid supplemented diets, the improvement in digestibility between intakes of 21 and 44 g $DM \cdot kg^{-.75} \cdot d^{-1}$ was slightly less than with the control diet (table III.4). Lasalocid at 36 $mg \cdot kg^{-1}$ DM had no significant effect ($P>.1$) on digestibility of energy or DM. N digestibility was

improved ($P<.05$) 4% by addition of lasalocid to the basal diet. Nitrogen digestibility declined with increasing feeding level. The trend was similar for both the control ($P<.05$) and the lasalocid supplemented ($P<.1$) diets (table III.4).

Energy losses in urine and methane are shown in table III.5. Because of problems with the respiration chamber cooling system, 12 observations (two lasalocid and two control animals at each of the fasting and at the 44 g $DM \cdot kg^{-.75} \cdot d^{-1}$ feeding level, and one lasalocid supplemented and one control at each of the 21 and 89 g $DM \cdot kg^{-.75} \cdot d^{-1}$ levels of intake) were excluded from calculations involving oxygen consumption and methane and carbon dioxide production.

Urinary energy loss as a percent of IE tended to decline ($P<.1$) with increasing feed intake. Percent DE lost as urinary energy declined ($P<.05$) in a quadratic manner with increasing feed intake for the control diet however there was no similar trend for the lasalocid supplemented diet. The decline was greatest between the 21 and 44 g $DM \cdot kg^{-.75} \cdot d^{-1}$ levels of intake. Percent DE lost in the urine was 35% greater at the lowest feeding level than at 44 g $DM \cdot kg^{-.75} \cdot d^{-1}$ (table III.5).

The percent IE lost as methane decreased ($P<.05$) as the intake was increased from 21 to 89 g $DM \cdot kg^{-.75} \cdot d^{-1}$ for both the lasalocid and control diets. When expressed as a percentage of DE, methane energy losses also decreased

($P<.05$) with increasing feed intake for the control diet. When the lasalocid supplemented diet was fed there was a tendency for a greater proportion of the DE to be lost as methane at the lower feeding levels. As a percent of DE, about 36% less energy was lost as methane when feed intake was increased from 21 to 44 g $DM \cdot kg^{-.75} \cdot d^{-1}$, whereas in the next incremental increase in feed intake only about 10% less energy was lost. With the last additional increment of feed the reduction in methane energy loss was about 19%. Methane production as a percentage of IE was not different ($P>.1$) between lasalocid and control diets, averaging 7.5 and 7.1%, respectively (table III.5). Lasalocid had no influence on urinary energy losses. When expressed as a percentage of DE, however, there was a trend for methane losses to be reduced ($P<.1$) with lasalocid supplementation.

Metabolizable energy (ME) content of both the lasalocid supplemented and control diets increased in a quadratic ($P<.05$) manner as feed intake increased, with the largest improvement between the two lowest feeding levels. The improvement in ME content of the control diet was about 20% when feed intake was increased from 21 to 89 g $DM \cdot kg^{-.75} \cdot d^{-1}$. Over the same range of feed intakes, the ME content of the lasalocid diet was improved by about 16%. Addition of lasalocid improved ($P<.05$) the average ME concentration of the diet by about 7% (2.73 vs. 2.91 for the control and lasalocid supplemented diets, respectively). Although the interaction between feeding level and ionophore

treatment was not significant ($P>.1$) it is of interest and potential importance. Lasalocid appeared to result in a larger increase in dietary ME concentration at the lower feeding levels than at the higher feeding levels.

The effects of feeding level and lasalocid on nitrogen balance are shown in table III.6. Fecal nitrogen losses increased ($P<.001$) with increasing feed intake for both the lasalocid supplemented and control diets. Nitrogen losses in the urine increased linearly with increasing feeding level for both the control ($P<.005$) and the lasalocid supplemented ($P<.001$) diets. Overall, when feed intake was increased from the lowest level to the highest, urinary nitrogen losses increased by 66% (table III.6). There was a linear increase ($P<.001$) in nitrogen retention with increasing feed intake in steers fed both the control and lasalocid supplemented diets. Lasalocid supplementation tended to reduce ($P<.1$) fecal nitrogen losses, however addition of lasalocid at 36 $mg \cdot kg^{-1}$ DM to the control diet did not influence urinary nitrogen losses which averaged 89.6 and 87.1 g nitrogen$\cdot d^{-1}$ for the lasalocid and control diets, respectively (table III.6). Also, lasalocid supplementation had no affect ($P>.1$) on the amount of nitrogen retained by steers fed the experimental diets.

The effect of feeding level and lasalocid on ME intake, heat production, energy retention and energy retained as protein are presented in table III.7. Lasalocid supplementation increased ($P<.05$) the ME intake by 6% for

steers consuming similar amounts of DM as those receiving the control diet. Heat production (HE) increased in a linear ($P<.005$) manner as ME intake increased in steers receiving the control diet. Lasalocid supplementation resulted in a quadratic ($P<.05$) increase in HE however, indicating that the increase in HE was progressively larger at higher feed intakes when the ionophore was fed. When averaged across feeding levels, lasalocid supplementation increased HE by approximately 6% (table III.7).

Increasing the feeding level of the control diet resulted in a linear increase ($P<.01$) in energy retention. Steers fed the lasalocid supplemented diet responded similarly, however, there was a trend for energy retention to increase in a quadratic ($P<.1$) manner. Overall, there was no difference in energy retention between the lasalocid and the control groups which averaged 20.8 and 19.4 $kcal \cdot kg^{-.75} \cdot d^{-1}$, respectively. Energy retained as protein, estimated from nitrogen retention, increased an average of 7 $kcal \cdot kg^{-.75} \cdot d^{-1}$ with each increase in feed intake from 21 to 89 $g\ DM \cdot kg^{-.75} \cdot d^{-1}$ and paralleled the changes in total energy retention (table III.7). Overall, lasalocid supplementation did not affect ($P>.1$) the amount of energy retained as protein (5.3 vs. 4.5 $kcal \cdot kg^{-.75} \cdot d^{-1}$ for the lasalocid and control cattle, respectively).

Net energy values, efficiency of energy utilization, estimated HeE, ME requirements for maintenance (MEm) and DM requirements for maintenance (DMm) are given in table III.8.

Regression equations, standard errors of estimate and correlation coefficients used to calculate the data in table III.8 are shown in tables III.9 and III.10. The linear and semilog-linear relationships are illustrated in figures III.1 and III.2. Addition of lasalocid to the basal diet increased estimated HeE 5 to 12%, however, only the values estimated by linear regression from below maintenance were significantly different ($P<.05$). Estimates of HeE from regression analysis (table III.8) were similar to those actually measured in fasting animals (table III.7).

Estimated DM required for maintenance (DMm) determined by linear regression above maintenance was reduced by 16% when lasalocid was included in the basal diet, but when estimated from below maintenance by linear regression the reduction in DMm was about 9%. Lasalocid supplementation did not appear to influence DMm, when the semilog-linear method of estimation was used. Estimated MEm values obtained from linear regression above and below maintenance were similar for both the control and lasalocid diets although the values estimated from above maintenance were slightly but not significantly larger than those estimated from below maintenance. Using the semilog-linear approach to estimate MEm from all intakes, or from above maintenance, there was a nonsignificant ($P>.1$) 4% increase in MEm with lasalocid supplementation (table III.8).

The partial efficiency of ME use for gain (kf) was determined as the slope of the linear regression of

$RE \cdot W^{-.75} \cdot d^{-1}$ on $ME \cdot W^{-.75} \cdot d^{-1}$ for intakes above maintenance (figure III.1). The addition of lasalocid to the basal ration had no effect (P>.1) on kf. Net energy for gain content of the diet (NEg), computed as the slope of the regression of $RE \cdot W^{-.75} \cdot d^{-1}$ on $DM \cdot W^{-.75} \cdot d^{-1}$ for intakes at maintenance and above, was also unaffected (P>.1) by lasalocid (table III.8).

Net energy for maintenance content of the diet (NEm) and the partial efficiency of ME use for maintenance (km) were computed similarly to NEg and kf using the incremental change in feeding between fasting and maintenance. Estimated km appeared to increase by 12% when lasalocid was added to the diet (table III.8; figure III.1). Estimated NEm of the ration containing supplemental lasalocid also appeared to improve by approximately 20% (table III.8), however in both cases the values were not significant (P>.1). NEm and km were also estimated by the method of Lofgreen and Garrett (1968) (table III.8). The km estimated by this method was lower than the km estimated by linear regression below maintenance and was not affected (P>.1) by lasalocid. NEm for the control diet computed by the Lofgreen and Garrett (1968) method was 11% less than the value determined by linear regression; the 10% improvement predicted by this method for the animals consuming the diet supplemented with lasalocid was not significant (P>.1) (table III.8).

The molar proportions of ruminal VFA are presented in table III.11. Increasing the feeding level resulted in a linear reduction ($P<.01$) in the proportion of acetate, an increase ($P<.05$) in the proportion of propionate and a linear decline ($P<.05$) in the ratio of acetate to propionate. No difference in the proportions of any of the VFAs could be detected ($P>.1$) when the diet was supplemented with 36 $mg \cdot kg^{-1}$ lasalocid, although the acetate to propionate ratio dropped from 4 to 2.5 (table III.11).

The effects of feeding level and lasalocid on plasma concentrations of insulin, glucagon, the insulin:glucagon ratio and growth hormone are shown in table III.12. Increasing the feeding level from 21 to 89 g $DM \cdot kg^{-.75} \cdot d^{-1}$ resulted in a three fold linear increase ($P<.001$) in the circulating levels of insulin. Insulin levels in both the control and lasalocid supplemented groups responded in a similar manner. Circulating levels of growth hormone declined linearly by almost 85% ($P<.005$) with increasing feed intake, with similar trends occuring in both treatment groups. Plasma glucagon levels were variable and not affected ($P>.1$) by feeding level. Increasing the feeding level of the 90% concentrate diet resulted in a linear increase ($P<.05$) of almost four fold in the insulin:glucagon ratio with the control diet but had no effect on this ratio when lasalocid was fed (table III.12). Addition of lasalocid to the basal diet tended to decreased ($P<.1$) the concentration of insulin in the plasma but had no

measureable effect on glucagon, growth hormone or the insulin:glucagon ratio.

D. DISCUSSION

Feedlot Performance

Overall, the addition of monensin and lasalocid to the 90% concentrate diet tended to increase ($P<.1$) feed efficiency and growth rate ($P=.12$) in feedlot heifers without a substantial decrease in feed intake. The magnitude of the response was greater for lasalocid supplementation than for monensin. Previous research indicates that the addition of monensin to feedlot cattle diets generally reduces feed consumption while causing little change in growth rate with a resulting improvement in feed efficiency (Raun et al.,1976; Boling et al., 1977; Pendulum et al., 1978; Hanson and Klopfenstein, 1979; Dyer et al., 1980). Lasalocid has also been found to generally reduce feed consumption, although not to the same extent as monensin, while causing either no change or an increase in growth rate and an improved feed efficiency (Davis, 1978; Bartley et al., 1979; Brethour, 1979; Brown and Davidovich, 1979; Kuhl et al., 1980; Berger et al., 1981b). The lack of a significant reduction in feed intake when monensin or lasalocid were added to the basal diet in this experiment is similar to the results reported by Cohen and Cooper (1983) feeding steers a 75% steam-rolled barley diet supplemented

with monensin. Willis and Boling (1982) and Berger et al. (1981b) also found no significant change in feed intake of steers fed high-concentrate corn-based diets supplemented with monensin or lasalocid.

The 10% improvement ($P<.1$) in feed efficiency of the heifers fed diets containing the two highest levels of lasalocid (36 and 54 $mg \cdot kg^{-1}$) is within the range of values reported in the literature for animals fed similar type diets supplemented with lasalocid (Brethour, 1979; Brown and Davidovich, 1979; Kuhl et al., 1980; Berger et al., 1981b). Monensin improved feed efficiency of the heifers by 6%. This value is similar to the mean improvement of 7.5% reported by Goodrich et al. (1984) from a summary of 228 trials involving over 11,000 head of cattle.

Compared to the control, neither monensin nor lasalocid significantly affected any of the carcass traits measured in this trial. These findings are in agreement with results reported by Heinemann et al. (1978), Dyer et al. (1980) and Cohen and Cooper (1983).

Influence of Feeding Level and Lasalocid on DE and ME

In experiment 2 the slight but nonsignificant ($P>.1$) increase in digestibility of IE, DM and N upon increasing feed intake from the lowest to the highest level was not expected. A decrease in digestibility of approximately 3% would have been predicted for this type of diet (ARC, 1980). The reason for this observed trend in digestibility is not

clear, however, it is likely due to the diet being made up largely of ground barley. This constituent has a relatively high rate of digestion in the rumen (Berger et al., 1981a), with only about 8% of it's organic matter digested in the lower gut (Garrett and Johnson, 1983), thus increased feed intakes are unlikely to result in a depression in starch digestion. Depressions in starch digestibility have been reported for nonsteam processed corn (Joanning et al., 1981) where 35 to 40% of the organic matter digestion occurs distal to the rumen.

The relative decline in the percent IE lost as methane with increasing feed intake seen in this trial has been well documented in the literature (Blaxter and Clapperton, 1965; Flatt et al., 1969; ARC, 1980). As a result of the higher percentage loss of IE in methane, urine and feces, ME content of the diet was depressed at the lowest feeding level. The absence of any effect of feeding level on ME between 44 and 89 g $DM \cdot kg^{-.75}$ feeding level with diets of high ME content is in agreement with literature reports (ARC, 1980).

Lasalocid had a slight positive, but nonsignificant effect on digestibility. In a review of the literature on the mode of action of monensin in the rumen, Schelling (1984) concluded that after an initial adaptation period, in which digestibilities are depressed, the ionophore resulted in a slight to moderate improvement in the digestibility of DM, energy and N. Berger et al. (1981b) feeding 30 and 45

$g \cdot ton^{-1}$ lasalocid, found no difference in DM digestibility by steers fed a high moisture, corn:corn silage diet. Paterson et al. (1983) using lambs also did not detect a change in digestibility of DM when lasalocid was added at the rate of 25 $mg \cdot lamb^{-1} \cdot d^{-1}$. The improvement in N digestibility (4%) is similar to the 4.6% increase in N digestibility observed by Ricke et al. (1983) and the 4 to 8% range of improvement reported by Paterson et al. (1983).

Ionophores cause a decreased rate of passage of ingesta through the digestive tract of animals (Schelling, 1984). This can change both the extent and site of digestion of dietary organic matter within the animal (Bartley et al., 1979; Paterson et al., 1983; Thivend and Jouany, 1983; Ricke et al., 1984). Muntifering et al. (1981) reported a slight depression in ruminal digestion of starch and crude protein but an increase in digestion of these components within the animal when a diet containing 90% whole shelled corn was supplemented with monensin at 33 $mg \cdot kg^{-1}$ diet. No measurements were made in this experiment to determine if this was one of the mechanisms by which lasalocid influenced feed efficiency.

The addition of lasalocid to the basal diet resulted in a nonsignificant decrease (5%) in methane production. The proportion of digested energy lost as methane also tended to be reduced (11%, $P<.1$) with lasalocid. Garrett (1982), with steers fed a high concentrate diet (10% acid detergent fiber) and supplemented with monensin, also reported that

the ionophore had no significant influence on methane production. Other in vivo studies, where high concentrate diets were supplemented with monensin, have resulted in depressions in methane production from 16 to 30% (Joyner er al., 1979; Thornton and Owens, 1981; Wedegaertner and Johnson, 1983). The explanation for this variation in effects of these ionophores on methane production remains unclear, however it may be due in part to an adaptation of the rumen microflora to the actions of these products (Wallace et al., 1981).

The percentage IE lost as urine was not affected ($P>.1$) by lasalocid. Wedegaertner and Johnson (1983) reported similar results for cattle fed a corn-corn silage diet supplemented with monensin.

Overall, lasalocid supplementation of the barley-based, high concentrate diet used in this experiment resulted in a 7% improvement ($P<.05$) in dietary ME. This is within the range of 5 to 8% improvement in ME reported by Thornton and Owens (1981) and Wedegaertner and Johnson (1983) when monensin was included in their basal rations. The improvement in dietary ME caused by addition of lasalocid was mainly due to improvements in digestibility of the diet which accounted for 85% of the difference in dietary ME. It is of interest that the percentage improvement in dietary ME appeared to be greater at lower feeding levels. This would indicate that a greater response with the ionophore may be obtained at lower feeding levels which agrees with

suggestions of Byers (1980).

The improvement in ME of the diet caused by lasalocid could explain a substantial proportion of the 10% improvement in feed efficiency of the heifers fed lasalocid supplemented diets in experiment 1. Using average ME values for control and lasalocid diets in the feedlot trials, calculated ME intakes were 23.5 and 24.4 Mcal·d^{-1} for control heifers and those fed lasalocid at 36 mg·kg^{-1} diet, respectively. The 0.9 Mcal·d^{-1} difference would be expected to correspond to about 0.1 kg·d^{-1} in gain for animals of this weight (NRC, 1984) which is about the difference which was measured between the two groups (table III.3). Thus, if no change in the energy requirements occurred, this change in ME would account for the response of the cattle to the ionophore. A similar conclusion was reached by Thornton and Owens (1981) who concluded that decreased fecal and methane losses explain the majority of the effects of ionophores on the feed efficiency in feedlot cattle.

Influence of Feeding Level and Lasalocid on Ruminal VFA

Increasing the feeding level of the high concentrate barley diet from the lowest to the highest feeding level resulted in a linear increase in the molar proportion of propionate and a linear reduction in the proportion of acetate in rumen fluid. Similar results were reported by Eadie and Mann (1970) feeding cattle a pelleted all-concentrate diet containing 85% barley. In their

experiment switching cattle from approximately 75% of ad libitum intake to ad libitum intake resulted in a shift in fermentation products from a low propionate to butyrate ratio to a higher ratio.

The molar ratio of acetate to propionate decreased nonsignificantly (P>.1) from 4.0 to 2.5 when lasalocid was included in the ration. This change is in agreement with other literature results, both in vitro and in vivo, which show that the addition of lasalocid increases the molar proportion of propionate and reduces the molar proportion of acetate and butyrate (Bartley et al., 1979; Brown and Davidovich, 1979; Fuller and Johnson, 1981; Ricke et al., 1984; Spears and Harvey, 1984). Possible reasons for the lack of statistical significance in the data are the small number of animals involved and the time after feeding that the samples were obtained. In order to minimize the stress of animal handling, rumen fluid samples were obtained just prior to the insertion of the jugular catheters, which was done immediately before the evening feeding. This occured approximately 8 h after the morning feeding. Whitelow et al. (1970), using heifers have shown that with high concentrate, barley-based diets VFA producion and total VFA concentration had returned to approximately prefeeding levels by 8 h after the last daily meal. In this light, it is possible that the reduced rate of fermentation and thus reduced VFA production at the time of sampling may have resulted in a variable effect of lasalocid on VFA molar

proportions in the rumen. A second reason for the large sample variability may have been inherent in the method of sampling rumen fluid. Samples were taken by stomach tube and thus may have been subjected to greater sampling error.

Energy Retention and Maintenance Requirements

In estimating dietary NE values, it is common practice to use an average dietary ME value, and apply this to all feeding levels (Garrett, 1976; Lofgreen, 1976; Byers, 1980; Wedegaertner and Johnson, 1983). However, Garrett (1982) has pointed out that in order to accurately estimate partial efficiencies above and below maintenance, and diet NEm and NEg by extrapolation, a precise estimate of dietary ME is essential. The ME value of a diet is most influenced by energy digestibility which normally declines with increasing intake (ARC, 1980), thus often ME content of the diet decreases with increasing intake (eg. Garrett, 1982; Wedegaertner and Johnson, 1983). If this occurs and a high ME value determined at maintenance is used for all feeding levels this will result in a low estimate of kf. Conversely use of the lower ME value determined at a high feeding level and applied to all feeding levels will lead to a high estimated kf. Calculated partial efficiency of ME use for maintenance will also be influenced. In this experiment, if the ME content of the diet was assumed to be 2.78 Mcal$\cdot$kg^{-1} (i.e. that determined at 44 g DM$\cdot$kg$^{-.75}\cdot$d^{-1}) for all feeding levels the estimated kf value for the control diet would be

0.52. This value is 9% less than the kf value for the control diet calculated using the actual ME content of the diet determined at each feeding level (table III.8). There was little difference between the km values determined by the two procedures.

Using ME values actually obtained at each feeding level, no difference was detected in the kf values for the control and lasalocid supplemented diets (table III.8; figure III.1). The nonsignificant 3.5% increase in NEg content of the lasalocid diet was thus caused by the difference in ME content of the diets. The observation that lasalocid had no effect on kf is consistent with results reported for cattle fed diets supplemented with monensin (Byers, 1980; Garrett, 1982; Wedegaertner and Johnson, 1983). That no change in kf values can occur when ruminal VFA changes are occurring is supported by several studies concerning the efficiency of utilization of various VFAs for gain. Bull et al. (1970), Johnson (1972), Johnson et al. (1974) and Ørskov et al. (1979) have demonstrated that mixtures of VFAs varying in acetate to propionate ratios within the physiological range observed in the rumen are used with equal efficiency for gain.

Energy requirements and utilization for maintenance are more difficult questions to deal with. As pointed out by Garrett (1982), the extrapolation procedure (log $HE \cdot W^{-.75}$ vs ME intake $\cdot W^{-.75}$) used by Lofgreen and Garrett (1968) to estimate HeE, then by manipulation NEm and km, is dependent

upon a precise estimate of the ME concentration of the diet. An inaccurate estimate of ME can thus result in biased estimates of HeE and NEm.

In this experiment when the semilog extrapolation procedure was used to estimate HeE for the control diet, with intakes above maintenance, the values determined were nearly identical to the measured value for the animals while fasting (table III.7). However when the same procedure was applied to the lasalocid diet, estimated HeE was about 5% less than the HeE measurements obtained with fasting animals but greater than the control value. Predicting fasting metabolism by linear regression from below maintenance also resulted in a higher ($P<.05$) estimate of HeE for the lasalocid supplemented group. Byers (1980) has proposed that the response in efficiency of cattle to ionophores is greater at or near maintenance and declines as the proportion of the diet utilized for gain increases. If this concept is correct, it would imply that measurements taken at several points above maintenance may not validly predict HE with an ionophore at or below maintenance when the extrapolation procedure is used.

Estimation of MEm from the linear regression of $RE \cdot W^{-.75}$ vs ME intake $\cdot W^{-.75}$ above maintenance (table III.8), gave slightly higher values for MEm than when estimated from below maintenance (table III.8; figure III.1). Using the semilog-linear approach, MEm values for cattle fed the lasalocid supplemented diet were increased by 3%. Pressman

(1973, 1976) has proposed that lasalocid is capable of changing a membrane's potential by altering its permeability to sodium and potassium. Such a change would necessitate an increased activity of the mechanisms which regulate intracellular ion concentrations and, in contrast to suggestions by Byers (1980) and Garrett (1982), would result in a greater energy expenditure for maintenance. It is known that some monensin is absorbed into the animal (Donoho, 1984) and it might be expected that lasalocid is as well. If so, it would contribute to an increased MEm and HeE in the animal.

Using the linear regression of $RE \cdot W^{-.75}$ vs DM intake$\cdot W^{-.75}$ for data below maintenance, the amount of DM required for maintenance (DMm) for the cattle fed the diets containing lasalocid was 9% lower than for cattle fed the control diet (table III.8). Extrapolating from above maintenance using the semilog-linear procedure yielded similar results although the magnitude of the difference was smaller (table III.8). It is now recognized that maintenance requirements are not constant and can change with increasing intake above maintenance (Turner and Taylor, 1983) thus it is useful to estimate DMm with a linear regression from data points above maintenance. This procedure predicted that cattle fed the lasalocid diet would require 16% less DM than control cattle to maintain energy equilibrium. Byers (1980) also calculated that monensin would decrease DMm requirements; increasing the ME content

of his monensin diet by 10% resulted in a 4% increase in MEm and a 5% decrease in DMm when these values were estimated by the semilog-linear procedure.

The improvement in NEm of the basal diet by lasalocid is in agreement with the findings of Wedegaertner and Johnson (1983) and is consistant with the effect of improved ME value of the diet on NEm shown by Byers (1980). Using the semilog-linear approach, km values estimated for the control and lasalocid supplemented diets were nearly the same and close to the value predicted by the NRC (1984) for diets where the ME content is around 3.0 Mcal·kg^{-1} DM. Estimating km by linear regression from below maintenance resulted in values for the control and lasalocid diets that were 11 and 24% higher, respectively, than the values estimated by the semilog-linear method. Blaxter (1967) reported an average km of .83 for cattle and sheep determined in 48 experiments which is similar to the values determined by linear regression from below maintenance in this experiment.

Influence of Feeding Level and Lasalocid on Hormones

Increased feed intake resulted in increased ($P<.001$) circulating levels of insulin and reduced ($P<.005$) circulating levels of growth hormone (table III.12) which is similar to results reported by Bassett et al. (1971), Bassett (1972), Trenkle (1978) and de Jong (1981). de Jong (1981), using goats, reported that energy intake had no

effect on plasma glucagon concentrations. In contrast, Bassett (1972) and Ostaszewski and Barej (1979) noted an increase in glucagon, in sheep, after feeding. Brockman (1982) has demonstrated that infusions of butyrate into the hepatic-portal vein at physiological concentrations significantly increased plasma glucagon levels, however infusions of propionate had no effect. In this study, in which a high concentrate diet was fed, large amounts of propionate would be expected to be absorbed from the rumino-reticulum and thus no response in glucagon levels would be expected.

Supplementation of the basal diet with lasalocid tended to cause a decrease ($P<.1$) in plasma insulin concentrations within the animals, with glucagon concentrations also being slightly reduced. It is well known that insulin and glucagon have major roles in the regulation of glucose homeostasis in ruminants (McDowell, 1983). Insulin appears to be a "storage hormone" (Brockman, 1978) facilitating the uptake of glucose, lipids and amino acids by peripheral tissue. Glucagon acts to balance this effect of insulin, promoting gluconeogenesis from amino acids and other glucose precursors and may also facilitate lipolysis in adipose tissue (McDowell, 1983). Further, it is known that feeding ionophores can increase glucose turnover rates (Van Maanan et al., 1978) and decrease amino acid utilization for gluconeogenesis (Beede et al., 1980). With this background it would be predicted that insulin concentrations would have

increased in response to the increased propionate absorption and greater ME intake when lasalocid was fed, which is the reverse of what tended to occur (table III.12). It is believed, however, that the molar ratio of insulin:glucagon is of more importance in controlling gluconeogenesis in ruminants than are the concentrations of either hormone alone (Bassett, 1975; McDowell, 1983). In our experiment molar ratios of insulin to glucagon were identical in control and lasalocid supplemented cattle (table III.12), which probably indicates that sufficient glucose precursors were available in both the control and lasalocid-fed cattle.

No changes in growth hormone concentrations due to lasalocid supplementation could be observed in this experiment. Trenkle (1978) has suggested that the role of growth hormone in metabolism is to mobilize energy from adipose tissue when the availability of dietary nutrients becomes limiting, especially when demands are increased above maintenance or when intake falls below that required for maintenance.

Conclusions

Heifers supplemented with lasalocid gained an average of 9.7% faster than control heifers and had a 9% improvement in feed efficiency. Comparable values for monensin-fed heifers were 4 and 6%, respectively. There was an overall 6.6% improvement in ME content of the diet with lasalocid with a nonsignificant trend for the improvement in ME to be

greater at lower feeding levels. The mechanism by which lasalocid improved the feed efficiency of cattle was through improving the ME content of the diet.

E. BIBLIOGRAPHY

Anonymous. 1978. Canada Agricultural Products Standards Act. Beef Carcass Grading Regulations. Canada Gazette Part II. 112(13):2945.

AOAC. 1980. Official Methods of Analysis (13th Ed.). Association of Official Analytical Chemists, Washington, DC.

ARC. 1980. The Nutrient Requirements of Ruminant Livestock. Agricultural Research Council. Commonwealth Agricultural Bureaux. Farnham Royal, Slough, England.

Bartley, E.E., E.L. Herod, R.M. Bechtle, D.A. Sapienze, B.E. Brent and A. Davidovich. 1979. Effect of monensin or lasalocid with or without niacin or amicloral, on rumen fermentation and feed efficiency. J. Anim. Sci. 49:1066.

Bassett, J.M. 1972. Plasma glucagon concentrations in sheep: their regulation and relation to concentrations of insulin and growth hormone. Aust J. Biol. Sci. 25:1277.

Bassett, J.M. 1975. Dietary and gastro-intestional control of hormones regulating carbohydrate metabolism in ruminants. In: I.W. McDonald and A.C.I. Warner (Eds.). Digestion and Metabolism in the Ruminant. p. 383. Sydney, Australia.

Bassett, J.M., R.H. Weston and J.P. Hogan. 1971. Dietary regulation of plasma insulin and growth hormone. Aust. J. Biol. Sci. 24:321.

Beede, D.K., G.T. Schelling, G.E. Mitchell, Jr. and R.E Tucker. 1980. Gluconeogenesis from threonine in growing goats abomasally administered glucose, propionate, oleate or fed monensin. J. Anim. Sci. 51(Suppl. 1):345.

Bergen, W.G. and D.B. Bates. 1984. Ionophores: Their effect on production efficiency and mode of action. J. Anim. Sci. 58:1465.

Berger, J., A.I. Rachlin, W.E. Scott, L.H. Sternbach and M.W. Goldberg. 1951. The isolation of three new crystalline antibiotics from Streptomyces. J. Am. Chem. Soc. 73:5295.

Berger, L.L., G.D. Anderson and G.C. Fahey, Jr. 1981a. Alkali treatment of cereal grains. 1. In situ and in vitro evaluation. J. Anim. Sci. 52:138.

Berger, L.L., S.C. Ricke and G.C. Fahey, Jr. 1981b. Comparison of two forms and two levels of lasalocid with monensin on feedlot cattle performance. J. Anim. Sci. 53:1440.

Blaxter, K.L. 1967. The Energy Metabolism of Ruminants. Hutchinson Scientific and Technical, London.

Blaxter, K.L. and J.L. Clapperton. 1965. Prediction of the amount of methane produced by ruminants. Brit. J. Nutr. 19:511.

Boling, J,A., N.W. Bradley and L.D. Campbell. 1977. Monensin levels for growing and finishing steers. J. Anim. Sci. 44:867.

Brethour, J.R. 1979. Lasalocid for finishing steers. J. Anim. Sci. 49(Suppl. 1):357.

Brockman, R.P. 1978. Roles of glucagon and insulin in the regulation of metabolism in ruminants. Can. Vet. J. 19:55.

Brockman, R.P. 1982. Insulin and glucagon responses in plasma to intraportal infusion of propionate and butyrate in sheep (*Ovis Aries*). Comp. Biochem. Physiol. 73A:237.

Brouwer, E. 1965. Report of subcommittee on constants and factors. Proc.of 3rd Int. Symp. on Energy Metab., European Assoc. Anim. Prod. Pub No. 11:441.

Brown, R.E. and A. Davidovich. 1979. The performance response to growing-finishing cattle fed graded levels of lasalocid. J. Anim. Sci. 49(Suppl. 1):358.

Bull, L.S., J.T. Reid and D.E. Johnson. 1970. Energetics of sheep concerned with utilization of acetic acid. J. Nutr. 100:262.

Byers, F.M. 1980. Determining effects of monensin on energy values of corn silage diets for beef cattle by linear or semi-log methods. J. Anim. Sci. 51:158.

Chen, M. and M.J. Wolin. 1979. Effect of monensin and lasalocid-sodium on the growth of methanogenic and rumen saccarolytic bacteria. Appl. Environ. Microbiol. 38:72.

Cohen, R.D.H. and J.A. Cooper. 1983. Avoparsin, monensin and zeranol for steers finishing on barley diets. Can. J. Anim. Sci. 63:361.

Davis, G.Y. 1978. Effects of lasalocid sodium on the performance of finishing steers. J. Anim. Sci. 47:(Suppl. 1):414.

de Jong, A. 1981. The effect of feed intake on nutrient and hormone levels in jugular and portal blood in goats. J. Agric. Sci. Camb. 96:643.

Dinnis, S.M., T.G. Nagaraja and E.E. Bartley. 1981. Effects of lasalocid or monensin on lactate-producing or using rumen bacteria. J. Anim. Sci. 52:418.

Donoho, A.L. 1984. Biological studies on the fate of monensin in animals and in the environment. J. Anim. Sci. 58:1528.

Dyer, I.A., R.M. Koes, M.L. Herlugson, L.B. Ojikutu, R.L. Preston, P. Zimmer and R. DeLay. 1980. Effect of avoparson and monensin on performance of finishing heifers. J. Anim. Sci. 51:843.

Eadie, J.M. and S.O. Mann. 1970. Development of the rumen microbial population: High starch diets and instability. In: A.T. Phillipson (Ed.) Physiology of Digestion and Metabolism in the Ruminant. pp 335-347. Oriel Press, New Castle-upon-Tyne.

Flatt, P.W., P.W. Moe, L.A. Moore and P.J. Van Soest. 1969. Estimation and prediction of the energy value of feeds for ruminants. EAAP Pub. No. 12. p. 59. Sept. Warsaw, Poland.

Fuller J.R. and D.E. Johnson. 1981. Monensin and lasalocid effects on fermentation in vitro. J. Anim. Sci. 53.1574.

Garrett, W.N. 1976. Influence of rumensin on energy utilization of corn and barley diets. 15th Annu. California Feeders Day 21:27.

Garrett, W.N. 1982. The influence of monensin on the efficiency of energy utilization by cattle. In: Proc. 9th Symp. on Energy Metab. Eur. Assoc. Anim. Prod. Pub. 29. pp. 104-17. Lillehammer, Norway.

Garrett, W.N. and D.E. Johnson. 1983. Nutritional energetics of ruminants. J. Anim. Sci. 57 (Suppl. 2):478.

Goodrich, R.D., J.E. Garrett, D.R. Gast, M.A. Kirick, D.A. Larson and J.C. Meiske. 1984. Influence of monensin on the performance of cattle. J. Anim. Sci. 58:1484.

Greenwood, F.C., W.M. Hunter, and J.S. Glver. 1963. Preparation of ^{125}I-labeled human growth hormone of high specific radioactivity. Biochem J. 89:114.

Guiterrez, F.C., L.M. Schake and F.M. Byers. 1982. Whole plant grain sorghum silage processing and lasalocid effects on stocker calf performance and rumen fermentation. J. Anim. Sci. 54:863

Hanson, T.L. and T.J. Klopfenstein. 1979. Monensin, protein source and protein level for growing steers. J. Anim. Sci. 48:474.

Heinemann, W.W., E.M. Hanks and D.C. Young. 1978. Monensin and tylosin in a high energy diet for finishing steers. J. Anim. Sci. 47:34.

Joanning, S.W., D.E. Johnson and B.W. Barry. 1981. Nutrient digestibility depressions in corn silage-corn grain mixtures fed to steers. J. Anim. Sci. 53:1095.

Johnson, D.E. 1972. Heat incriment of acetate and corn and effects of casein infusions with growing lambs. J. Nutr. 102:1093.

Johnson, D.E., J.T. Reid, L.S. Bull and J. Robb. 1974. Observations on the efficient utilization of acetic acid above maintenance by sheep. In: Proc. 6th Symp. on Energy Metab. Eur. Assoc. Anim. Prod. Pub. 14. p. 43.

Joyner, A.E., L.J. Brown, T.J. Fogg and J.T. Rossi. 1979. Effect of monensin on growth, feed efficiency and energy metabolism of lambs. J. Anim. Sci. 48:1065.

Kuhl, G.L., M. Esser, M.E. Bergeland and L.B. Embry. 1980. Efficiency of lasalocid with solar-dried, acid-treated, and ensiled shelled corn finishing rations. J. Anim. Sci. 51(Suppl 1):376.

Laarveld, B., D.E. Kerr and R.P. Brockman. 1986. Effects of growth hormone in glucose and acetate metabolism in sheep. Comp. Biochem. Physiol. 83A:499.

Lofgreen, G.P. 1976. A comparison of sodium bicarbonate with Rumensin in a finishing ration. 15th Annu. California Feeders Day 15:20.

Lofgreen G.P. and W.N. Garrett. 1968. A system for expressing net energy requirements and feed values for growing and finishing beef cattle. J. Anim. Sci. 27:793.

McDowell, G.H. 1983. Hormonal control of glucose homeostasis in ruminants. Proc. Nutr. Soc. 42:149.

Muntifering, R.B., B. Theurer and T.H. Noon. 1981. Effects of monensin on site and extent of whole corn digestion and bacterial protein synthesis in beef steers. J. Anim. Sci. 53:1565.

NRC. 1984. Nutrient Requirements Of Domestic Animals, No 4. Nutrient Requirements of Beef Cattle. Sixth Revised Ed. National Academy of Sciences - National Research Council, Washington, DC.

Ørskov, E.R., D.A. Grubb, J.S. Smith, A.J.F. Webster and W. Corrigall. 1979. Efficiency of utilization of volatile fatty acids for maintenance and energy retention by sheep. Brit. J, Nutr. 41:541.

Ostaszewski, P. and W Barej. 1979. Influence of rumen fermentation rate on glucose and insulin blood levels. Annals de Recherches Veterinaires. 10:385.

Paterson, J.A., B.M. Anderson, D.K. Bowman, R.L. Morrison and J.E. Williams. 1983. Effect of protein source and lasalocid on nitrogen digestibility and growth by ruminants. J. Anim. Sci. 57:1537.

Pendulum, L.C., J.A. Boling and N.W. Bradley. 1978. Levels of monensin with and without tylosin for growing-finishing steers. J. Anim. Sci. 47:1.

Pressman, B.C. 1973. Properties of ionophores with broad range cation selectivity. Fed. Proc. 32:1698.

Pressman, B.C. 1976. Biological applications of ionophores. Ann. Rev. Biochem. 45:501.

Raun, A.P., C.O. Cooley, E.L. Potter, R.P. Rathmacher and L.F. Richardson. 1976. Effect of monensin on feed efficiency of feedlot cattle. J. Anim. Sci. 43:670.

Ricke, S.C., L.L. Berger, P.J. van der Aar and G.C. Fahey, Jr. 1984. Effect of lasalocid and monensin on nutrient digestion, metabolism and rumen characteristics of sheep. J. Anim. Sci. 58:194.

Schelling, G.T. 1984. Monensin mode of action in the rumen. J. Anim. Sci. 58:1518.

Spears, J.W. and R.W. Harvey. 1984. Performance, ruminal and serum characteristics of steers fed lasalocid on pasture. J. Anim. Sci. 58:460.

Steel R.D.G. and J.H. Torrie. 1980. Principals and Procedures of Statistics. A Biometrical Approach. (2nd Ed.). McGraw-Hill Book Co. New York.

Thivend, P. and J.P. Jouany. 1983. Effect of lasalocid sodium on rumen fermentation and digestion in sheep. Reprod. Nutr. Develop. 23:817.

Thonney, M.L., E.K. Heide, D.J. Duhaime, R.J. Hand and D.J. Perosis. 1981. Growth, feed efficiency and metabolite concentrations of cattle fed high forage diets with lasalocid or monensin supplements. J. Anim. Sci. 52:427.

Thornton ,J.H. and F.N. Owens. 1981. Monensin supplementation and in vivo methane production by steers. J. Anim. Sci. 52:628.

Trenkle, A. 1978. Relation of hormonal variation to nutritional studies and metabolism of ruminants. J. Dairy Sci. 61:281.

Turner, H.G. and C.S. Taylor. 1983. Dynamic factors in models of energy utilization with particular refrence to maintenance requirement of cattle. Wld. Rev. Nutr. Diet. 42:135.

Van Maanan, R.W., J.H. Herbein, A.D. McGilliard and J.W. Young. 1978. Effects of monensin on in vivo rumen propionate production and blood glucose kinetics in cattle. J. Nutr. 108:1002.

Wallace, R.J., J.W. Czerkawski and G. Brekenridge. 1981. Effects of monensin on the fermentation of basal rations in the Rumen Simulation Technique (Rusitec). Brit. J. Nutr. 46:131.

Wedegaertner, T.C. and D.E. Johnson. 1983. Monensin effects on digestibility, methanogenesis and heat increment of a cracked corn-silage diet fed to steers. J. Anim. Sci. 57:168.

Whitelaw, F.G., J. Hyldgaard-Jensen, R.S. Reid and M.G. Kay. 1970. Volatile fatty acid production in the rumen of cattle given an all-concentrate diet. Brit. J. Nutr. 24:179

Willis, C.M. and J.A. Boling. 1982. Level of protein with and without monensin for finishing steers fed at controlled intake. Nutr. Rep. Int. 25:399.

Young, B.A., B. Kerrigan and R.J. Christopherson. 1975. A versatile respiratory pattern analyser for studies of energy metabolism of livestock. Can. J. Anim. Sci. 55:17.

TABLE III.1. EXPERIMENTAL DIET.[a]

Ingredient	IFN	% of diet
Alfalfa-grass hay	1-00-294	10.0
Barley, dry rolled	4-00-549	81.5
Canola meal	5-03-871	3.0
Molasses, wet beet	4-00-668	1.8
Calcium carbonate, 38% Ca	6-01-069	0.9
Calcium phosphate, 15-18% Ca; 21% P	6-01-082	0.2
Trace mineralized salt[b]		0.35
Vitamin-selenium premix[c]		0.25
Additive premix[d]		2.0

[a] Air-dry basis.

[b] Trace mineralized salt contained 96.5% NaCl; 0.4% Zn; 0.16% Fe; 0.12% Mn; 0.033% Cu; 0.007% I; 0.004% Co.

[c] Vitamin-selenium premix provided 5000 IU vitamin A; 825 IU vitamin D and 5 IU vitamin E, per kg total diet along with 0.075 mg per kg of selenium (as sodium selenite).

[d] Formulated to provide 0, 24.2, 36.3, and 54.2 mg of lasalocid per kg of dry matter in four diets and 11 mg monensin per kg dry matter for the first 28 days and 33 mg·kg^{-1} for the remainder of the feeding period in the fifth diet.

TABLE III.2. COMPOSITION OF DIETS CONTAINING 90% CONCENTRATE.

	Control	Monensin	Lasalocid (mg·kg⁻¹ DM)			SE[b]
			24	36	54	
Dry matter, %	89.3	89.5	89.4	88.9	89.0	.38
Crude protein[a]	12.3	12.0	12.5	12.1	12.1	.34
Calcium[a]	.57	.56	.55	.53	.60	.12
Phosphorus[a]	.41	.40	.42	.40	.42	.02

[a] Percent of dry matter.

[b] Standard error of the mean for dry matter was based on four replicates whereas three replicates were analysed for crude protein, calcium and phosphorus.

TABLE III.3. EFFECT OF IONOPHORES ON FEEDLOT PERFORMANCE AND CARCASS CHARACTERISTICS OF HEIFERS.

			Lasalocid (mg·kg⁻¹ DM)			
	Control	Monensin	24	36	54	SE[a]
No. heifers	20	20	20	20	20	
Initial wt, kg	308	309	310	309	306	1.75
Final wt, kg	430	436	444	442	441	3.49
Daily gain, kg						
0-28 days	1.16[c]	1.32[cd]	1.28[cd]	1.19[c]	1.46[d]	.05
28-70 days	1.48	1.38	1.55	1.56	1.40	.07
70-98 days	.97	1.15	1.16	1.21	1.24	.09
Overall	1.24	1.29	1.36	1.35	1.37	.04
Daily DM consumption, kg						
0-28 days	7.3	6.9	7.3	7.4	7.3	.34
28-70 days	9.1	8.8	9.1	8.8	9.0	.26
70-98 days	9.0	9.2	9.6	8.9	9.0	.36
Overall	8.6	8.4	8.8	8.4	8.5	.28
DM·gain⁻¹, kg						
0-28 days[b]	6.3[c]	5.3[de]	5.7[cd]	6.2[c]	5.0[e]	.18
28-70 days	6.1	6.6	5.9	5.7	6.5	.40
70-98 days	9.5[f]	8.1[fg]	8.3[g]	7.4[g]	7.5[g]	.49
Overall	6.9[f]	6.5[fg]	6.4[g]	6.2[g]	6.2[g]	.17
Carcass characteristics						
Warm carcass wt, kg	231	235	240	241	238	4.30
Dressing percent	53.6	54.0	54.1	54.5	54.1	.35
Rib eye area, cm	60.2	63.0	64.0	62.8	62.7	1.51
Fat depth, cm	1.38	1.39	1.42	1.52	1.39	.08
Grade						
Canada B1	1					
Canada A1	3	8	4	2	2	
Canada A2	13	6	12	13	15	
Canada A3	3	5	3	5	3	
Canada A4		1	1			
No. abcessed livers	8	12	10	9	10	

[a] Standard error of the mean.

[b] The percentage hay in the diet for the first 28 d period averaged 26.6, 25.8, 25.9 and 26.2% for these five diets, respectively.

[cde] Means in the same row with different superscripts are significantly different (P<.05).

[fg] Means in the same row with different superscripts are significantly different (P<.1).

TABLE III.4. EFFECT OF FEEDING LEVEL AND LASALOCID ON DIET DIGESTIBILITY.

Item	Feeding level[a]				Treatment	SE[b]	
	21	44	67	89	Mean	Level	Treatment
No. observations	8	8	8	8	16		
Weight of steers, kg							
Control	627	609	612	608	614	10.4	3.1
Lasalocid	625	623	620	602	618		
Mean	626	616	616	605			
Dry matter intake, $g \cdot kg^{-.75} \cdot d^{-1}$							
Control	22.1	44.2	66.7	89.0	55.5	1.1	.1
Lasalocid	22.2	44.1	66.6	88.9	55.4		
Mean	22.2	44.4	66.6	89.0			
Dry matter digestibility, %							
Control[c]	67.8	77.1	75.6	77.8	74.6	2.6	1.1
Lasalocid[d]	70.9	76.8	79.1	78.1	76.2		
Mean[d]	69.4	76.9	77.3	78.0			
Energy digestibility, %							
Control[c]	66.5	76.9	75.2	77.3	74.0	2.9	1.2
Lasalocid[d]	70.2	76.9	79.0	77.9	76.0		
Mean[d]	68.4	76.9	77.1	77.6			
Nitrogen digestibility, %							
Control[c]	79.2	82.0	75.8	74.7	77.9	1.5	1.2
Lasalocid[d]	83.3	81.8	81.0	78.1	81.0[e]		
Mean[d]	81.3	81.9	78.4	76.4			

[a] g DM·kg$^{-.75}$·d^{-1}.

[b] Standard error of mean for feeding level and treatment.

[c] Linear feeding level effect (P<.05).

[d] Linear feeding level effect (P<.1).

[e] Different from control (P<.05).

TABLE III.5. EFFECT OF FEEDING LEVEL AND LASALOCID ON ENERGY LOSS IN URINE AND METHANE AND DIETARY ENERGY CONTENT.

Item	Feeding level[a]				Treatment Mean	SE[b]	
	21	44	67	89		Level	Treatment
No. observations	8	8	8	8	16		
Energy losses, % of IE[c]							
Urine							
Control	4.8	3.5	2.8	2.8	3.5	.2	.1
Lasalocid	4.4	3.3	3.0	3.8	3.6		
Mean[j]	4.6	3.4	2.9	3.3			
Methane[e]							
Control[lm]	9.6	8.0	5.9	6.6	7.5	.5	.3
Lasalocid[l]	10.2	7.0	6.2	5.1	7.1		
Mean[g]	9.9	7.5	6.0	5.8			
Energy losses, % of DE[d]							
Urine							
Control[fk]	7.3	4.6	3.8	3.7	4.8	.5	.4
Lasalocid	6.2	4.3	3.8	4.8	4.8		
Mean[j]	6.8	4.4	3.8	4.3			
Methane[e]							
Control[i]	14.2	10.6	7.9	8.6	10.3	.6	.4
Lasalocid[hm]	13.8	8.8	7.9	6.4	9.2[o]		
Mean[gl]	14.0	9.7	7.9	7.5			
Digestible energy, Mcal·kg^{-1} DM							
Control[gm]	2.87	3.32	3.24	3.35	3.19	.11	.05
Lasalocid[im]	3.05	3.34	3.43	3.38	3.29		
Mean[j]	2.96	3.33	3.34	3.36			
Metabolizable energy, Mcal·kg^{-1} DM							
Control[fl]	2.31	2.78	2.85	2.88	2.73	.07	.04
Lasalocid[gl]	2.50	3.00	3.00	2.99	2.91[n]		
Mean[fk]	2.40	2.89	2.93	2.93			

[a] g DM·kg$^{-.75}$·d^{-1}.
[b] Standard error of mean for feeding level and treatment.
[c] Intake energy.
[d] Digestible energy.
[e] No. observations for methane energy losses: 2, 3, 4, 3 for feeding levels 21, 44, 67 and 89; respectively.
[fghij] Linear feeding level effect (P<.001), (p<.005), (P<.01), (P<.05), (P<.1); respectively.
[klm] Quadratic feeding level effect (P<.005), (P<.05), (P<.1); respectively.
[no] Different from control (P<.05), (P<.1).

TABLE III.6. EFFECT OF FEEDING LEVEL AND LASALOCID ON NITROGEN BALANCE.

Item	Feeding level[a]				Treatment	SE[b]	
	21	44	67	89	Mean	Level	Treatment
No. observations	8	8	8	8	16		
Nitrogen intake, $g \cdot d^{-1}$							
Control	55.5	110.6	167.0	223.3	139.1	1.0	.2
Lasalocid	55.3	110.0	165.5	221.0	137.9		
Mean	55.4	110.4	166.3	222.1			
Fecal nitrogen, $g \cdot d^{-1}$							
Control[c]	11.5	20.0	40.5	56.3	32.1	.9	.4
Lasalocid[c]	9.3	20.0	31.5	48.5	27.3[e]		
Mean[c]	10.4	20.0	36.0	52.4			
Urinary nitrogen, $g\ d^{-1}$							
Control[d]	67.3	76.8	95.6	108.8	87.1	1.6	.8
Lasalocid[c]	62.5	81.8	108.3	106.5	89.6		
Mean[d]	64.9	79.3	102.0	107.6			
Nitrogen retained, $g\ d^{-1}$							
Control[c]	-23.3	14.0	30.8	58.3	19.9	1.5	.7
Lasalocid[c]	-16.5	8.3	25.8	66.0	20.9		
Mean[c]	-19.9	11.1	28.3	62.1			

[a] $g\ DM \cdot kg^{-.75} \cdot d^{-1}$.

[b] Standard error of mean for feeding level and treatment.

[c] Linear feeding level effect ($P<.001$).

[d] Linear feeding level effect ($P<.005$).

[e] Different from control ($P<.1$).

TABLE III.7. EFFECT OF FEEDING LEVEL AND LASALOCID ON PARTITIONING OF METABOLIZABLE ENERGY.

	Feeding level[a]					Treatment	SE[b]	
Item	0	21	44	67	89	Mean	Level	Treatment
No. observations	4	6	4	8	6	14		
ME intake, kcal·kg$^{-.75}$·d^{-1}								
Control[c]	0.0	49.9	119.8	191.3	254.3	123.1	4.2	2.4
Lasalocid[c]	0.0	52.2	134.9	201.7	265.7	131.0[j]		
Mean[c]	0.0	51.2	127.4	196.5	260.0			
Heat production, kcal·kg$^{-.75}$·d^{-1}								
Control[d]	65.5	73.3	96.7	131.9	151.0	103.7	3.5	2.0
Lasalocid[cg]	72.7	76.4	106.4	129.1	166.1	110.1[j]		
Mean[cg]	69.1	74.9	101.5	130.5	158.5			
Energy retention, kcal·kg$^{-.75}$·d^{-1}								
Control[e]	-65.5	-23.5	23.1	59.4	103.3	19.4	4.8	2.7
Lasalocid[ch]	-72.7	-23.9	28.5	72.6	99.6	20.8		
Mean[c]	-69.1	-23.7	25.8	66.0	101.4			
Energy retained as protein, kcal·kg$^{-.75}$·d^{-1}								
Control[f]		-6.2	1.5	8.7	14.2	4.5	1.7	1.1
Lasalocid[chi]		-4.9	2.6	7.3	16.1	5.3		
Mean[d]		-5.6	2.1	8.0	15.1			

[a] g DM·kg$^{-.75}$·d^{-1}.

[b] Standard error of mean for feeding level and treatment.

[cdef] Linear feeding level effect (P<.001), (P<.005), (P<.01), (p<.1); respectively.

[gh] Quadratic feeding level effect (P<.05), (P<.1); respectively.

[i] Cubic feeding level effect (P<.05).

[j] Different from control (P<.05).

TABLE III.8. ENERGY PARTITIONING BY STEERS FED A 90% CONCENTRATE, BARLEY-BASED DIET WITH OR WITHOUT LASALOCID DETERMINED BY LINEAR AND SEMILOG-LINEAR METHODS.

Item	No. of Observations	Linear[a]		Semilog-linear[b]	
		Control	Lasalocid	Control	Lasalocid
Estimated fasting heat production, HeE in kcal·W$^{-.75}$·d^{-1}					
From above maintenance	9			65.6	69.3
From below maintenance	5	65.1 ± 1.6	72.8 ± 3.1*	64.2	69.2
From all intakes	14			63.7	68.5
Estimated maintenance requirements					
Dry matter, g·W$^{-.75}$·d^{-1}					
From above maintenance	9	31.5	26.4	32.8	31.8
From below maintenance	5	36.7	33.4		
From all intakes	14			32.0	31.4
Metabolizable energy, kcal·W$^{-.75}$·d^{-1}					
From above maintenance	9	83.6	81.2	89.7	92.5
From below maintenance	5	79.5	78.8		
From all intakes	14			87.3	91.5
Efficiency of ME utilization, %					
Maintenance, km[c]		.82 ± 0.44	.92 ± 0.08	.73	.75
Gain, kf	9	0.57 ± 0.06	0.58 ± 0.04		
Net energy content of feeds, kcal·g^{-1}					
NEm[c]		1.79 ± .19	2.17 ± .26	1.98	2.18
NEg	9	1.71 ± .27	1.77 ± .17		

[a] Energy was partitioned by separate linear regression above and below maintenance.

[b] Energy was partitioned by the method of Lofgreen and Garrett (1968).

[c] Number of observations used in the linear regression were 5 and in the semilog-linear regressions were 14.

* Different from control (P<.05).

TABLE III.9. LINEAR RELATIONSHIPS BETWEEN RETAINED ENERGY (RE) WITH METABOLIZABLE ENERGY (ME) AND DRY MATTER (DM) INTAKE FOR CATTLE FED THE HIGH CONCENTRATE BARLEY-BASED DIET WITH OR WITHOUT LASALOCID AT 36 MG·KG^{-1} DM.

Treatment	Estimating equations	Number of observations	Standard error of estimate	Correlation coefficient
	Below maintenance			
kcal RE·W$^{-.75-1}$ (Y) vs. kcal ME·W$^{-.75-1}$ (X)				
Control	Y = -65.108 + .819X	5	2.290	.99
Lasalocid	Y = -72.758 + .923X	5	4.412	.99
kcal RE·W$^{-.75-1}$ (Y) vs. g DM·W$^{-.75-1}$ (X)				
Control	Y = -65.599 + 1.786X	5	4.636	.98
Lasalocid	Y = -72.593 + 2.174X	5	6.269	.98
	Above maintenance			
kcal RE·W$^{-.75-1}$ (Y) vs. kcal ME·W$^{-.75-1}$ (X)				
Control	Y = -47.908 + .573X	9	8.068	.97
Lasalocid	Y = -46.973 + .578X	9	6.131	.98
kcal RE·W$^{-.75-1}$ (Y) vs. g DM·W$^{-.75-1}$ (X)				
Control	Y = -53.523 + 1.709X	9	11.619	.93
Lasalocid	Y = -47.602 + 1.769X	9	8.440	.97

TABLE III.10. SEMILOG RELATIONSHIPS BETWEEN HEAT PRODUCTION (HE)[a] AND METABOLIZABLE ENERGY INTAKE (ME)[a] FOR CATTLE FED THE HIGH CONCENTRATE BARLEY-BASED DIET WITH OR WITHOUT LASALOCID AT 36 MG·KG^{-1} DM.

Treatment	Estimating equation	Number of observations	Standard error of estimate	Correlation coefficient
	Below maintenance			
log HE·W$^{-.75-1}$ (Y) vs. ME·W$^{-.75-1}$ (X)				
Control	Y = 1.814 + .00112X	5	.0142	.93
Lasalocid	Y = 1.861 + .00045X	5	.0258	.51
	Above maintenance			
log HE·W$^{-.75-1}$ (Y) vs. ME·W$^{-.75-1}$ (X)				
Control	Y = 1.817 + .00151X	9	.0286	.95
Lasalocid	Y = 1.840 + .00136X	9	.0188	.97
	All intakes			
log HE·W$^{-.75-1}$ (Y) vs. ME·W$^{-.75-1}$ (X)				
Control	Y = 1.804 + .00157X	14	.0238	.99
Lasalocid	Y = 1.836 + .00137X	14	.0250	.99

[a] HE and ME are expressed in kcal.

TABLE III.11. EFFECT OF FEEDING LEVEL AND LASALOCID ON RUMEN VFA CONCENTRATIONS[a].

Item	Feeding level[b]					Dietary treatment		
	21	44	67	89	SE[c]	Control	Lasalocid	SE
No. steers	4	3	4	4		8	7	
Total, $umol \cdot ml^{-1}$	53.1	69.4	81.3	60.8	8.31	75.3	55.2	5.03
Proportions								
Acetate[d]	71.4	65.4	62.2	54.4	2.72	65.0	61.2	3.46
Propionate[e]	16.5	19.3	27.7	36.1	3.89	21.7	29.4	5.26
Butyrate	12.1	15.3	10.1	9.5	1.57	13.3	9.5	1.8
Acetate:Propionate[e]	4.7	3.7	2.5	2.5	.58	4.0	2.5	.91

[a] $Mol \cdot 100\ mol^{-1}$.

[b] $g\ DM \cdot kg^{-.75} \cdot d^{-1}$.

[c] Standard error of the mean.

[d] Linear feeding level effect ($P<.01$)..

[e] Linear feeding level effect ($P<.05$).

TABLE III.12. EFFECT OF FEEDING LEVEL AND LASALOCID ON PLASMA HORMONE CONCENTRATIONS.

Item	Feeding level[a]				Treatment	SE[b]	
	21	44	67	89	Mean	Level	Treatment
No. observations	8	8	8	8	16		
Insulin, $ng \cdot ml^{-1}$							
Control[d]	1.7	3.0	4.1	5.9	3.7	.6	.1
Lasalocid[f]	1.7	3.1	3.1	4.8	3.2[h]		
Mean[c]	1.7	3.0	3.6	5.4			
Glucagon, $pg \cdot ml^{-1}$							
Control	242	370	195	242	262	44	17
Lasalocid	197	262	237	224	230		
Mean	219	316	216	233			
Insulin:glucagon ratio, $mol \cdot mol^{-1}$							
Control[f]	4.4	5.0	15.4	15.7	10.6	3.5	1.5
Lasalocid	11.4	8.1	8.8	14.1	10.6		
Mean[f]	7.9	6.6	12.1	14.9			
Growth hormone, $ng \cdot ml^{-1}$							
Control[g]	5.4	1.4	1.2	.8	2.2	.7	.8
Lasalocid[e]	3.4	3.0	.9	.6	2.0		
Mean[d]	4.4	2.2	1.0	.7			

[a] g $DM \cdot kg^{-.75} \cdot d^{-1}$.
[b] Standard error of mean for feeding level and treatment.
[c] Linear feeding level effect (P<.001).
[d] Linear feeding level effect (P<.005).
[e] Linear feeding level effect (P<.01).
[f] Linear feeding level effect (P<.05).
[g] Linear feeding level effect (P<.1).
[h] Different from control (P<.1).

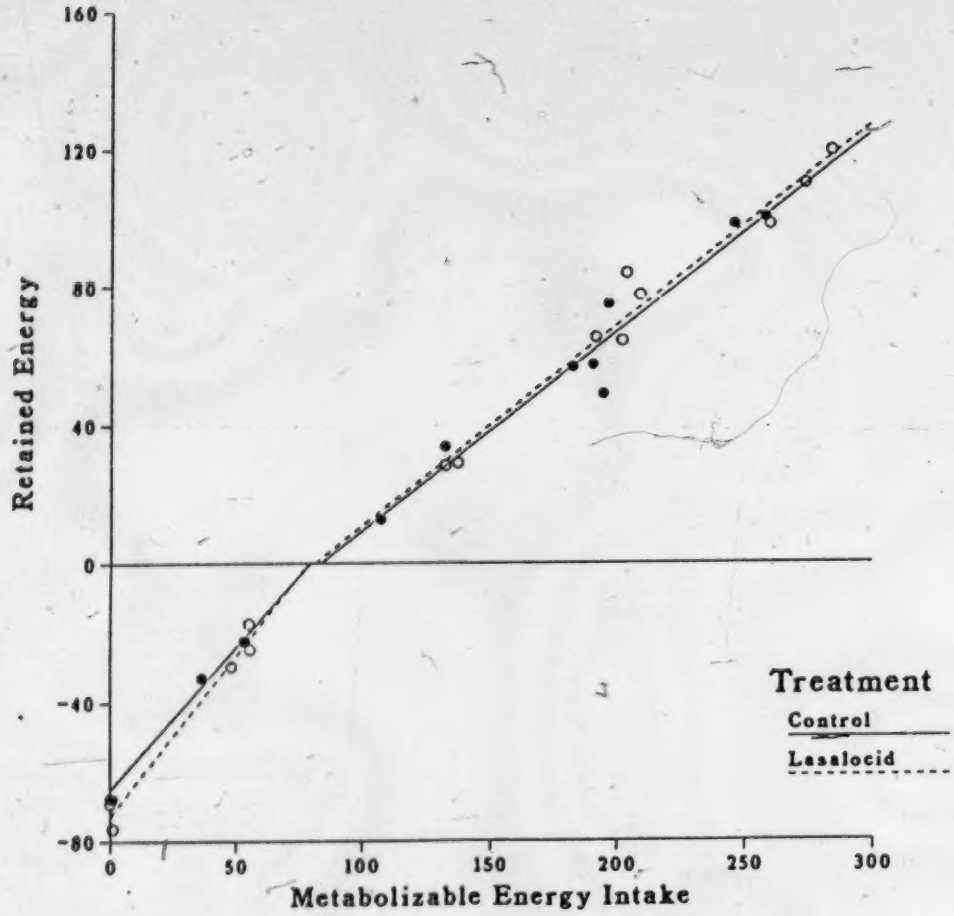

Figure III.1 Relationship between retained energy ($kcal \cdot kg^{-.75} \cdot d^{-1}$) and metabolizable energy intake ($kcal \cdot kg^{-.75} \cdot d^{-1}$) for control and lasalocid steers.

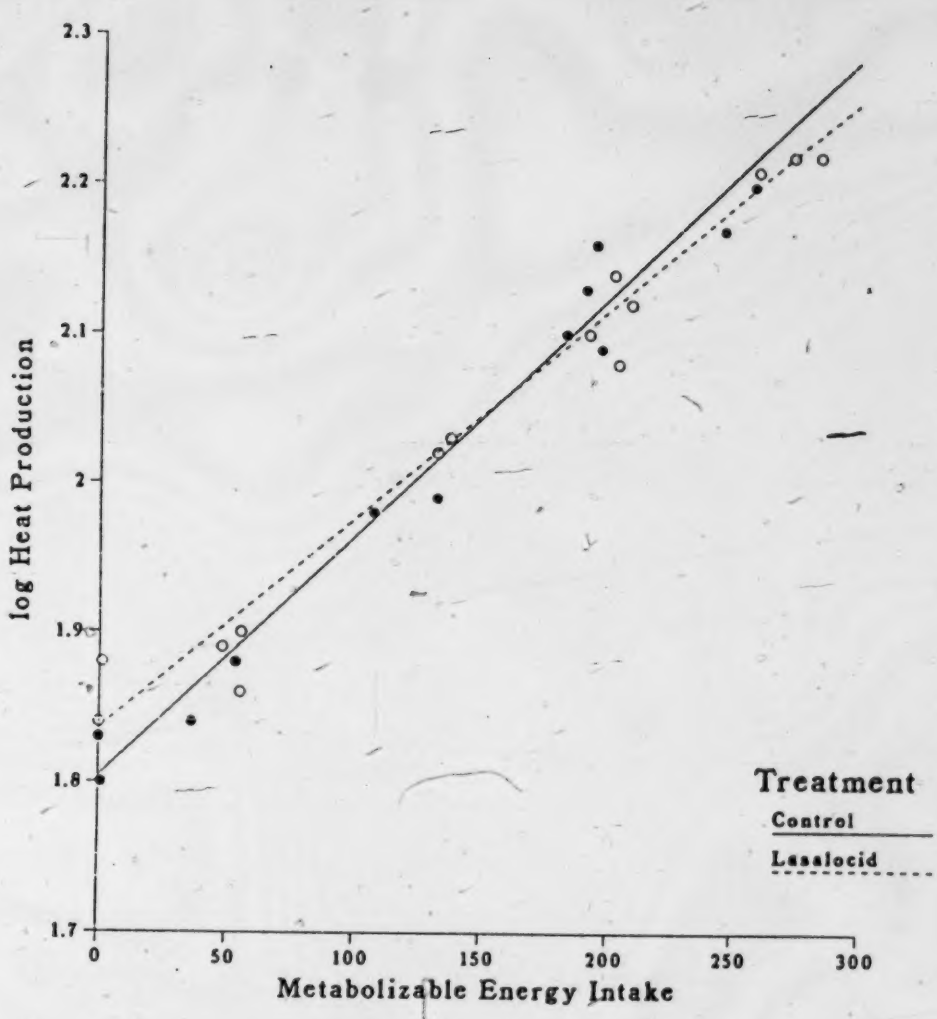

Figure III.2 Relationship between log heat production ($kcal \cdot kg^{-.75} \cdot d^{-1}$) and metabolizable energy intake ($kcal \cdot kg^{-.75} \cdot d^{-1}$) for control and lasalocid steers.

IV. EFFECTS OF ENVIRONMENT ON THE ENERGETIC EFFICIENCY OF FEEDLOT STEERS.

A. INTRODUCTION

Cattle show marked seasonal fluctuations in their level and efficiency of production (Young, 1981). When exposed to adverse winter conditions feed efficiency may be reduced 14 to 20% and growth rate may be depressed by as much as 30% because less feed energy is available for productive processes (Elam, 1970; Webster, 1970; Knox and Handley, 1973; Milligan and Christison, 1974; Ames et al., 1975; Johnson and Crownover, 1975).

Numerous hormonal and adaptive changes combine to cause the reduced productive efficiency of ruminants raised in cold environments. With the onset of winter the animal begins to adapt to increasingly colder temperatures by gradually increasing its resting metabolic rate (Christopherson and Young, 1986). In animals fully acclimated to winter conditions heat production may be increased 30 to 40% (Webster et al., 1970; Slee, 1971; Young, 1975a,b; Young and Christopherson, 1974). This results in an increased energy requirement for maintenance.

A second factor which can affect productive efficiency is the increase in metabolic rate which occurs during acute cold stress when the environmental temperature drops below the lower critical temperature of the animal. For feedlot cattle the estimated increase in resting metabolic rate is

approximately 2 $kcal \cdot kg^{-.75} \cdot d^{-1}$ for each degree that the environmental temperature falls below the animals lower critical temperature (Christopherson and Young, 1986).

There is also an increased rate of passage of digesta in cold exposed animals which leads to reduced digestive efficiency. The magnitude of the decline in digestibility of ruminant diets in the cold can be as much as 0.2 digestibility units per degree drop in environmental temperature below 20°C depending on the type of diet and the degree of cold stress on the animal (Colditz and Kellaway, 1971; Warren et al., 1974; Christopherson, 1976; Westra and Christopherson, 1976; Kennedy and Milligan, 1978; Nicholson et al., 1980).

It would be expected that the above factors would mainly influence the availability of dietary energy for gain. Previous work (Suleiman and Mathison, 1979) has shown a considerable reduction in the net energy for gain (NEg) value of barley-based rations fed to steers during the winter when compared to the same diet fed to steers during summer trials. Net energy for maintenance (NEm) values were affected similarly, although not to the same extent. These authors concluded that the depression in digestibility due to the cold winter temperatures could explain only a small part of the decrease in NEg values observed in their trial and attributed the lower NEg value to a greater proportion of energy retained as protein in the cold. Unfortunately the results from this experiment are somewhat confounded

since different animals and feeds were used over the experimental periods.

The objective of the present experiments was to examine the effect of a cold environment on the NE values of a barley-based diet and thus on the performance and efficiency of energy use of growing feedlot cattle.

B. MATERIALS AND METHODS

Experiment 1

The digestibility and metabolizability of the all-concentrate diet (table IV.1) were determined at feeding levels of approximately 50 and 80 g DM·kg$^{-.75}$·d^{-1}. Four steers (481 kg) of mixed breeding (predominantly Hereford and Angus plus varying ammounts of Galloway, Limousin and Charolais), housed in a thermoneutral environment and previously adapted to metabolism crates and a confinement-type respiration chamber, were utilized in a cross-over design so that each steer was fed at both levels of intake. Each of the two experimental periods consisted of a 10 d adaptation period to the respective feeding level. This was followed by a 7 d period during which a total collection of feces and urine was made, and then by a 24 h period in which methane production measurements were made. Steers were fed twice daily throughout the experiment.

Methane production was measured for each animal with an open-circuit calorimetery system which was previously

described in Chapter III of this thesis. The daily energy lost as methane was computed as the total methane produced ($l \cdot d^{-1}$ at standard temperature and pressure) x 9.45 $kcal \cdot l^{-1}$ methane (Brouwer, 1965).

Aliquots of daily fecal output were collected and stored at -20 C. At the end of each 7 d collection period the feces samples were dried at 60 C, ground and pooled to yield individual animal composites which were stored at -20 C for later analysis. Daily urine output was collected in plastic tubs which contained 100 ml of 5N HCl with 1 $g \cdot l^{-1}$ mercuric chloride. A composite sample for each animal was stored at -20 C for later analysis.

DM content of the feed and feces was determined by oven drying at 110 C to a constant weight. Nitrogen in the feed, feces and urine was determined by the standard macro-Kjeldahl procedure (AOAC, 1980). Gross energy content of the feed, feces and urine was determined in an automatically controlled Parr adiabatic bomb calorimeter[4].

Digestible energy (DE) and ME values were calculated from the combustible energy of the diet corrected for the appropriate energy losses. Energy values for the barley grain were calculated assuming that molasses provided 3.48 and 2.86 Mcal of DE and ME $\cdot kg^{-1}$ DM (NRC, 1984).

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[4]Parr Instrument Co. Moline, IL.

Experiment 2

Steers were fed either indoors or outdoors at one of three different feeding levels to assess the influence of Alberta winter weather on energy partitioning and the net energy values of a barley-based diet. Forty nine Hereford and Hereford-cross yearling steers were purchased in December 1979 from a local commission firm for this experiment. Upon arrival animals were ear-tagged; vaccinated for blackleg and malignant edema and given a 2 ml intramuscular injection containing 1000000, 300000 and 100 IU of vitamins A, D and E respectively. No growth promotant implants were used. Prior to the start of the experimental feeding period the cattle were offered alfalfa-grass hay and 2 kg barley· $head^{-1} \cdot d^{-1}$.

For establishment of the initial slaughter group the steers were separated into seven groups according to liveweight. One steer from each weight group was randomly chosen and slaughtered at the start of the feeding period to establish the initial body composition. The remaining 42 animals were then randomly allotted to one of two locations (indoor or outdoor) and one of three feeding levels within each location. This yielded seven animals per feeding level in each location. The length of the feeding period was between 92 and 106 d, at which time the steers were sent to slaughter.

The 21 indoor cattle were assigned to three pens (4.5 by 5 m) in an environmentally controlled, slatted-floor

(concrete slats were 10.2 cm wide with 3.8 cm openings) confinement barn so that each pen contained at least two animals per feeding level. No bedding was used for these steers. The outdoor group were divided similarly and kept in three open pens (8 by 8 m) which had a 3.6 m 20% porosity fence on the north side but no overhead shelter. Wood shavings were used for bedding for these steers. Water was continuously available from heated water bowls in each pen.

Steers were fed an all-concentrate diet (table IV.1). Assigned feeding levels were 50, 65 and 80 g dry matter (DM)$\cdot kg^{-.75} \cdot d^{-1}$, with the amount of feed offered adjusted weekly according to changes in liveweight. Steers were individually restrained in stanchions, within their pens, twice daily and offered one-half of their daily allotment at each feeding. Samples of the diet were taken at regular intervals during the experimental period and stored at -20 C for later analyses.

Temperature and relative humidity were monitered on a daily basis for the indoor group of steers using a continuously recording hygrothermograph''. Meterological data for the outdoor group of steers during the experimental period were obtained from the Government of Canada Atmospheric Service at the Edmonton International Airport which is within 10 km of the experimental site (Environment Canada, 1980). Previous experience has shown that environmental conditions were very similar between the two

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''Model C-8368-00. Cole-Parmer Instrument Co. Chicago, IL.

locations. No attempt was made to measure any environmental parameters other than temperature and relative humidity.

Initial and final weights were averages of weights taken on three consecutive days. Steers were weighed every week throughout the trial. All weights were taken after feed and water had been withheld for approximately 16 h.

The animals which completed the test were sent to slaughter at a local abattoir in three groups of 12 and one group of six over a 14 d period. The groups of 12 animals were formed by randomly choosing two animals from each feeding level within each location. The group of six was composed of the remaining steers. The trial was terminated in this manner because the cold storage facilities at the University of Alberta Meats Lab were only large enough to handle 12 half carcasses at one time. After overnight chilling the carcasses were graded and ribeye and back fat depth (average at top, middle and bottom of the ribeye between the 11th and 12th rib) were measured by Agriculture Canada personel (Anonymous, 1978). Dressing percentages were calculated on the basis of warm carcass weight and final ~~feedlot~~ weight.

The left half of each carcass was delivered to the University of Alberta Meats Lab. Each half carcass was separated into a front and hind quarter. The quarters were weighed in air and then reweighed while submerged in a tank of water which was cooled to 4 C. Care was taken to remove any air which might have been trapped in the carcass during

immersion in the water. Carcass specific gravity was then calculated as the carcass weight in air divided by the difference of the carcass weight in air and it's weight in water. Empty body weight, composition and energy content were estimated from carcass specific gravity by the method of Garrett and Hinman (1969). The energy content of the fat and fat-free dry matter of the whole empty body were taken as 9.385 and 5.539 $kcal \cdot g^{-1}$ respectively (Garrett and Hinman, 1969).

The initial energy content of the steers fed throughout the feeding trial was estimated as the initial liveweight of the animal times the average energy content ($Mcal \cdot kg^{-1}$ liveweight) of the initial slaughter group. Retained energy (RE) was then the difference between initial and final energy content. Heat production (HE) was estimated as total ME intake minus RE. Metabolizable energy required for maintenance (MEm) was estimated separately for each location, as the point at which ME intake was equal to HE, from the regression of log HE on ME intake (Lofgreen and Garrett, 1968) using an average of the ME content of the diet determined at two feeding levels. Fasting heat production (HeE) was estimated separately for each location by extrapolation of the regression of log HE on ME intake to the point where ME intake equals zero. Multiple regression analysis was used to partition ME intake among either maintenance, protein or fat deposition for the indoor and outdoor groups separately using Model One of Old and Garrett

(1985). The NEm of the diet, for each location, was estimated from the amount of DM required to maintain the animal in energy equilibrium (Lofgreen and Garrett, 1968). The NEg of the ration was estimated as the slope of the regression of retained energy (RE) on DM intake within each location.

Statistical Analyses

Mean values for data from experiment 1 were compared using analysis of variance techniques with level of intake being tested against level of intake by animal interaction (Steel and Torrie, 1980). Individual animal data from experiment 2 were analysed by two-way analysis of variance with location and level of intake as sources of variation. Feeding level means were tested for linear and quadratic effects by orthogonal comparisons. There were no significant location by level of intake interactions. Statistical differences between NE values obtained from regression equations were determined according to procedures given in Steel and Torrie (1980).

C. RESULTS

Experiment 1

Energy losses in the feces, urine and methane as well as the DE and ME values of the complete diet measured in the metabolism trial, and the DE and ME values calculated for barley grain are presented in table IV.2. Increasing the

feed intake from approximately 1.3 to 2.0 times maintenance did not affect the percent IE lost in feces ($P>.1$). The proportion of IE lost in urine declined from 7.4% of IE at the low feeding level to 5.0% at the high feeding level, however the values were not significantly different ($P>.1$). There was a 19% reduction ($P<.05$) in the loss of the combustible energy intake (IE) as methane with increasing feeding level, with methane losses being 7.0 and 5.7% of IE for steers fed 54 and 82 g DM$\cdot kg^{-.75}\cdot d^{-1}$, respectively (table IV.2). The overall effect of increasing feeding level was a nonsignificant ($P>.1$) increase in the ME content from 2.79 Mcal$\cdot kg^{-1}$ DM at the low intake to 2.93 Mcal$\cdot kg^{-1}$ DM at high intake.

Experiment 2

Information on environmental conditions during the winter feeding trial are summarized in table IV.3. Indoor temperatures remained fairly constant averaging 16.9 ± 2.7 C over the experimental period. Relative humidity also remained constant averaging 76.4 ± 4.7 percent. Winter weather summaries from previous years suggest that environmental conditions during the experimental period for the outdoor group were nearly normal for that time of year (Suleiman and Mathison, 1979).

The steers remained healthy throughout the experimental period, however some problems were encountered with feed intake; not all steers readily consumed their assigned

ration, particularly at the high feeding level. Thus, for the purpose of comparing the results from the feeding trial, data from two steers in the high feeding level, indoor group and one steer in the high feeding level, outdoor group were removed prior to statistical analysis of the data in tables IV.4, IV.5, IV.6 and IV.7 since their feed intake deviated more than 10% from the others in their respective groups. All animals were included in the regressions of log HE on ME intake (table IV.8 and figure IV.1) and in the multiple regressions used to partition ME for protein and fat gain.

Feedlot performance data are summarized in table IV.4. As expected, with increasing feed intake, steers grew faster ($P<.001$), were more efficient ($P<.001$) and were heavier ($P<.001$) at the end of the trial. This resulted in heavier carcasses ($P<.001$) and more fat covering ($P<.05$) with increasing feed intake.

Carcass data are summarized in table IV.5. Steers fed 64 and 70 g $DM \cdot kg^{-.75} \cdot d^{-1}$ had more fat covering ($P<.05$) in both the indoor and outdoor groups and the rib-eye area was increased ($P<.05$) in the outdoor group at higher intakes when compared to steers fed 52 g $DM \cdot kg^{-.75} \cdot d^{-1}$. Dressing percentage was not significantly ($P>.1$) influenced by increasing feed intake.

Effects on empty body parameters closely followed liveweight and carcass trends with respect to feeding level (table IV.6 and IV.7). As DM intake increased, there was a linear increase in gain in estimated empty body weight

(P<.001), energy stored as protein (P<.005) and fat (P<.05), and total energy retained (P<.005). These trends resulted in steers having heavier estimated final empty body weights (P<.005), slightly more empty body protein (P<.1) and empty body fat (P<.1) and more energy in the empty body (P<.05) with increasing feed intake.

Location (indoor or outdoor) had major effects on feedlot performance (table IV.4). Steers housed indoors had 0.22 kg higher average daily gains (P<.001) and 51% better feed conversion efficiencies (P<.001) than the outdoor group even though feed intakes were similar. These differences resulted in indoor steers having heavier carcasses (P<.001), more fat covering (P<.001) and higher dressing percentages (P<.001) than outdoor steers (table IV.5).

Steers kept outdoors had higher carcass specific gravities (P<.001, table IV.6) and lighter estimated final empty body weights (P<.005) than steers kept indoors. Estimated daily gains in empty body weight were 2.2 times higher (P<.001) for the indoor group as compared with the outdoor group (table IV.7). Daily empty body energy gain of the indoor steers was 2.8 times that of the outdoor steers (P<.001). Indoor steers gained approximately twice as much energy as protein (P<.005) and three times as much energy as fat (P<.001) as the outdoor steers.

The estimated net energy maintenance requirement, which is equivalent to the fasting metabolism, was increased (P<.01) by 18% in the steers exposed to the cold winter

environment (table IV.8). MEm for the indoor steers was 101 $kcal \cdot kg^{-.75} \cdot d^{-1}$ when estimated by the method of Lofgreen and Garrett (1968). The MEm of 142 $kcal \cdot kg^{-.75} \cdot d^{-1}$ for the outdoor group of steers was 41% higher ($P<.01$) than for the indoor group. These were similar to the values of 104 and 140 $kcal \cdot kg^{-.75} \cdot d^{-1}$ estimated by multiple regression for the indoor and outdoor cattle, respectively. As a result, the amount of DM needed to meet the maintenance energy requirements (DMm) was increased ($P<.01$) from 35.2 to 49.5 $g \cdot kg^{-.75} \cdot d^{-1}$ (table IV.8).

The NEm value of the barley grain for the indoor group was 1.96 $Mcal \cdot kg^{-1}$ DM. The NEm value for barley estimated for the outdoor group was 1.64 $Mcal \cdot kg^{-1}$ DM which is approximately 16% lower than that determined for the inside group. Efficiencies of ME use for maintenance (k_m) were 0.64 and 0.55 for the indoor and outdoor steers, respectively (table IV.8). The NEg content of the barley grain DM determined for the indoor group was 1.37 $Mcal \cdot kg^{-1}$. The NEg value determined with steers exposed to the outdoor environment was 0.81 $Mcal \cdot kg^{-1}$ DM which was 41% lower ($P<.01$) than that determined for the indoor group. Corresponding efficiencies of use of ME for gain (k_f) were 0.45 and 0.27% for the indoor and outdoor groups respectively (table IV.8). Estimates of efficiency of ME use for protein and fat synthesis did not differ between indoor and outdoor groups (table IV.8).

D. DISCUSSION

Digestibility and Metabolizability of the All-Concentrate Diet

The results of the present trial indicate that the energy digestibility of the all-concentrate barley-based diet fed to steers, in a thermoneutral environment, was not affected by an approximate 50% increase in DM intake. These findings are in contrast with the majority of the experimental results which have been reported. Tyrrell and Moe (1975) concluded, after an extensive review of the literature, that increasing intake is related to a significant depression in digestibility of a wide variety of diets containing various grains, roughages and supplements in many combinations. On average this depression amounts to four percentage units per multiple of maintenance increase in intake. Similar findings were reported by Van Es and Honing (1979) who showed depressions in energy digestibility of up to seven percentage units per multiple of maintenance in dairy cows. The ARC (1980) predicts a decline in digestibility of from three to eight percent for the intake differences in this experiment, depending on the quality of the diet, with lower quality diets showing the largest effect.

Digestibility of feeds is inversely related to rate of passage and directly proportional to rate of digestion (Van Soest, 1982), so digestibility of dietary components with a

relatively fast rate of passage or a slow rate of digestion or both will be affected most by increasing intake. All-concentrate diets, particularly those based on barley grain, have a high rate of digestion of organic matter in the rumen relative to the rate of passage of dietary material (Kennedy et al., 1982). Starch makes up approximately 65% of the barley DM (Waldo, 1973). Thivend and Vermorel (1971), Waldo (1973) and Berger et al. (1981) reported that barley starch is more readily attacked than starch from wheat, corn or sorghum and observed that about 94% of the barley starch is digested in the rumen with very little variation occuring due to processing method or to changing DM intake. Thus, although depressions in digestibility at higher intake occurs with most diets, a reduction in digestibility with increasing intake might not be expected for the type of diet fed in this experiment. Data reported in Chapter III of this thesis, in fact, confirm the lack of significant influence of feeding level between 1.0 and 2.0 times maintenance on DM digestibility with a similar diet.

Increasing the level of intake resulted in a small, nonsignificant ($P>.1$), increase in the ME content of the diet. Similar results were reported in Chapter III of this thesis and haveeen obtained by other reseachers. Tyrrell and Moe (1974) reported that the ME value of their corn silage-based diet supplemented with barley was not influenced by increasing intake from maintenance to three

times maintenance even though energy digestibility was depressed by 3.7% per multiple of maintenance. This demonstrates a partial compensation for digestibility depression from lower methane and urine energy losses. Blaxter and Clapperton (1965), Blaxter et al. (1966) and Flatt et al. (1969) have shown that the reduction in energy losses in methane and urine averaged 12 and 10 kcal·Mcal^{-1} gross energy consumed, respectively, for each unit increase in feeding level.

Feedlot Performance, Carcass Characteristics and Empty Body Parameters

Location had major effects on feedlot performance. Steers housed indoors grew 49% faster and had 51% better feed conversion efficiencies than the outdoor steers even though feed intakes were the same. Similar results have been reported by Milligan and Christison (1974) in Saskatchewan. Their study, of monthly records on a total of 1,970 steers over a seven year period, showed that exposure to the cold winter environment reduced feed efficiency by almost 50%. Average daily gain was reduced by 30% in animals fed in the cold even though feed intake was not restricted.

Results from trials housing cattle indoors vs those kept outdoors and exposed to a colder environment show similar trends. Bennett and O'Mary (1965) compared two groups of animals, one housed in a barn and the other kept

in an open lot. Average daily gains (ADG) for the housed group were 34% higher at ad libitum feeding levels. Data of Hidiroglou and Lessard (1971) in Quebec show similar trends. Feed consumption was similar between indoor and outdoor groups, however, the outdoor cattle grew 31% slower and were 30% less efficient in converting feed to liveweight gain.

Muhamed et al. (1983) investigated the effect of diet, housing and season on the performance of feedlot cattle in Iowa. ADG were 1.12 vs. 1.05 $kg \cdot d^{-1}$ for the summer and winter steers, respectively (6% difference) even though dry matter intakes were similar (8.3 vs. 8.15 $kg \cdot d^{-1}$ for the summer and winter periods, respectively).

Christopherson (1985), from a literature survey, estimated that 1.5 Mcal ME $\cdot head^{-1} \cdot d^{-1}$ could be saved by providing overhead shelter to cattle gaining 1 $kg \cdot d^{-1}$ in the winter. If an insulated barn were provided the increase in daily energy savings was estimated to be an additional 2.5 Mcal $\cdot head^{-1} \cdot d^{-1}$.

The influence of cold in reducing carcass weights and fat of the outdoor steers in this trial agree with the results reported by Nour et al. (1981) from a study using Angus steers housed in a heated, slatted floor barn or in partially covered outdoor pens. Their results show that the steers housed indoors accumulated more fat and similar amounts of muscle in their carcasses when fed at equal intakes and slaughtered at the same liveweight. Numerous studies have shown that, at similar slaughter weights,

faster growing cattle have more carcass fat and higher dressing percentages than the same type of animal on a restricted energy intake and growing at a slower rate (Callow, 1961; Hendrickson et al., 1965; Hiner and Bond, 1971; Byers, 1980).

The effect of the cold environment on the growth rate of the steers in this trial is particularly evident in the empty body gain data. Estimated daily gains in empty body weight, energy retained as fat and protein and total energy retained were substantially higher for the indoor group as compared to the outdoor group. The proportion of the total energy retained as fat in the indoor steers (86%) was greater than in the outdoor steers (78%). Similar results were demonstrated by Suleiman and Mathison (1979). Cattle fed during the 1974/75 winter period gained less energy and proportionately less energy as fat than similar animals fed during the 1974 summer feeding period. This trend was particularly evident at the high feeding level.

The data from this study indicate that the differences in carcass and empty body composition between the indoor and outdoor groups of steers can be explained by the reduced growth rate which resulted in changes in the composition of empty body gain and different final empty body composition. It is well documented that faster growing animals retain more fat at similar carcass and empty body weights regardless of the type of diet (Byers, 1980). However, it is also possible that cold may influence body composition

through hormonal changes which occur in animals during adaptation to cold environmental temperatures. Prolonged cold exposure elevates plasma levels of thyroxine and triiodiothyronine in cattle (Christopherson and Thompson, 1983). Elevated thyroid hormone can directly stimulate protein synthesis and can act in a permissive role, creating an environment in which other hormones can more effectively influence metabolic processes (Martin, 1976; Sasaki and Weekes, 1986). Thyroid hormone can also potentiate the lipolytic response of catecholamines (Martin, 1976; Sasaki and Weekes, 1986) which are also elevated in the cold (Christopherson et al., 1978).

Maintenance Energy Requirements of Steers

It is generally recognized that the variation in the efficiency of energy use for maintenance is small when comparisons are made using nonproducing animals in conditions of thermoneutrality (Moe and Tyrrell, 1973). However when animals are subjected to chronic cold exposure, hormonal and metabolic changes occur which increase maintenance energy expenditure (Young, 1981) and may influence the efficiency with which energy is used for maintenance processes (Gregg and Milligan, 1982; Sasaki and Weekes, 1986; Christopherson and Thompson, unpublished). Data of Webster et al. (1970) for growing cattle and Young (1975a,b) for adult cattle demonstrate that resting metabolic rate, or fasting metabolism, is increased 30 to

40% as a result of physiological acclimation to several weeks of cold exposure. Similar changes were seen in this trial, with the estimated fasting metabolism of steers exposed to cold winter temperatures increasing by 18%.

The MEm requirement of the outdoor group of steers was increased by 41% over the indoor group. The large increase in MEm relative to the change in fasting metabolism during cold exposure would indicate a change in metabolism occurred as the animals attempted to maintain homeothermy in the face of increasing heat loss to the environment. There are numerous mechanisms which tend to increase heat production in cold adapted animals. During acute cold exposure the adult ruminant's primary source of thermogenesis is shivering (Sasaki and Weekes, 1986). However, as the duration of cold exposure lengthens, shivering intensity declines in cattle (Young, 1975a). Thus shivering may only contribute minimally to increased heat production during chronic cold exposure. The decrease in shivering is associated with an increase in thermoneutral heat production from other sources. The results of Graham and Christopherson (1981) indicate that a form of catacholamine-stimulated nonshivering thermogenesis (NST) may occur in ruminants which is different from the classical NST which occurs in response to norepinephrine in small animals which possess brown adipose tissue(Sasaki and Weeks, 1986). The mechanism of increased heat production in NST has not been fully resolved, however, an increase in plasma

membrane Na^+/ K^+ ATPase activity may make a major contribution (Gregg and Milligan, 1982). Cold exposure may increase protein degradation in cattle (Thompson and Christopherson, unpublished). This may be an indication of an increased rate of muscle protein turnover which would also contribute to increased heat production. Other metabolic processes may also be contributing to the increased thermoneutral heat production in cold adapted animals however they as yet have not been characterized.

The efficiency of ME use for maintenance apparently declined from 64 to 55% (table IV.8) in animals exposed to a cold environment. This resulted in a corresponding 16% decrease in NEm of the diet. The reasons for this decrease cannot be determined from this experiment since calculated dietary NEm values are dependent upon the estimated heat increment of feeding above maintenance, ME content of the diet and estimated fasting heat production. For a given ME content of the diet, predicted NEm content will decrease if NEg is decreased (NRC, 1984).

Influence of the Cold Environment on the Efficiency of Energy use for Gain.

In this experiment there was little variation in estimated HE of the outdoor steers at similar ME intakes but a large variation was observed in the indoor group (figure IV.1). The reason for this is not clear, however it may have been due to an insufficient amount of essential

nutrients, such as dietary crude protein, for support of maximum growth. For example, Blaxter and Boyne (1978) reported that at a constant metabolizability, when dietary protein content decreased from 200 to 50 $g \cdot kg^{-1}$ organic matter, kf declined from 0.58 to 0.50%. The influence of a potential nutrient deficiency would be less apparent in the outdoor group because they had a slower growth rate and thus would have a lower requirement for dietary nutrients such as protein (Ames et al. 1980).

The NEg value of 1.37 $Mcal \cdot kg^{-1}$ DM for barley grain obtained with the indoor animals agrees with the NEg value of 1.29 $Mcal \cdot kg^{-1}$ DM estimated from the equation relating NEg to ME determined by Garrett (1980b) and used by the NRC (1984). The NEg of the diet was decreased by 41% when it was fed to the outdoor steers which indicates that a single NEg value for feeds cannot be validly used with animals in different environments.

The efficiency with which ME is used for tissue deposition, kf, has been considered to be mainly a function of the ME content of the diet (ARC, 1980; NRC,1984), thus a possible explanation of the low NEg is that the ME content of the diet decreased markedly in the cold. Depressions in DM digestibility due to cold temperatures have been well documented for forage-based diets (Christopherson, 1976; Westra and Christopherson, 1976; Kennedy et al., 1976, 1977, Kennedy and Milligan, 1978, Nicholson et al., 1980; Kennedy, 1985). A large decrease in dietary ME in the outdoor group

of steers was very unlikely in this experiment, however, since Kennedy et al. (1982) established that temperature had no influence on digestibility of a rapidly fermented, all-concentrate diet in wethers. Similar results have been reported for an all-concentrate diet fed to lambs (McBride, 1982) and a pelleted barley-alfalfa diet fed to wethers (Young and Degan, 1981). Metabolizability of all concentrate diets may even be slightly improved in the cold. Kennedy and Milligan (1978) reported that ruminal methane production was reduced by 30% when the same diet was fed to cold exposed sheep as compared to sheep fed in a warm environment. Thus some factor other than a decreased ME content of the diet must have been responsible for the lower kf and NEg values for the diet fed to the outdoor steers.

In this regard, there was a significant ($P<.05$) relationship between the amount of tissue deposited in the animal and energetic efficiency in this trial (table IV.8). Multiple regression analyses indicated that the efficiency of ME use for tissue growth by the steers ranged from 71 to 91% for fat and 11 to 13% for protein with no significant effect ($P>.1$) due to location. Since outdoor steers deposited proportionately more of their energy as protein than the indoor steers (21 vs 14%), differences in efficiency of tissue deposition could explain the low kf value in the outdoor steers. Therefore, kf is dependent on the relative efficiencies of protein and fat deposition and is thus more a function of the physiological state of the

animal than of the type of diet.

Differences in efficiency of fat and protein deposition have also been reported by others. Old and Garrett (1985), using similar techniques, have estimated that fat deposition in growing and finishing beef cattle is between five and six times more energetically efficient than is protein deposition. Their estimates of the efficiency of ME use for tissue growth are 49 to 58% for fat and 10 to 11% for protein deposition depending on the model used. Byers (1982) estimated the efficiency of ME use for fat deposition to be in the range of 60 to 70% and for protein deposition to vary between 10 and 40%. Geay (1984) estimated values of 75 and 20% for the energetic efficiency of fat and protein deposition respectively. However, there is a need for caution in attaching biological significance to efficiencies estimated by the regression approach when the independent variables (protein gain and fat gain) are highly correlated (Garrett, 1980a). In this regard the apparent low efficiencies of protein synthesis are difficult to explain on a theoretical basis. Van Es (1978) estimated, that in ruminants, the theoretical maximum biochemical efficiency of fat synthesis would be 80% and protein synthesis about 85%. Similar estimates of efficiency for fat (76%) and protein (86%) synthesis were reported by Baldwin and Smith (1974). However, synthesis of protein and fat is not synonymous with deposition since deposition is the net result of synthesis and degradation. The cost of deposition must thus also

include the costs of synthesis, degradation and turnover rather than just the cost of synthesis (Garrett and Johnson, 1983).

Conclusions

The results of this experiment indicate that animal performance, whether measured as liveweight gain or empty body weight gain, is adversely affected by decreasing temperature when feed intake is held constant. As a consequence of a greater proportion of retained energy being deposited as protein in the cold exposed steers, estimated dietary NE values were substantially reduced when compared to the values estimated for the same diet fed to steers in the warm environment or calculated from the ME content of the diet. Caution should thus be used in estimating the net energy content of diets fed to cattle raised in cold environments using the current methods of calculation.

E. BIBLIOGRAPHY

Ames, D.R., D.R. Brink and R.R. Schalles. 1975. Relationship of ambient temperature and ADG. J. Anim. Sci. 41:262 (Abstr.).

Ames, D.R., D.R. Brink and C.L. Willms. 1980. Adjusting protein in feedlot rations during thermal stress. J. Anim. Sci. 50:1.

Anonymous. 1978. Canada Agricultural Products Standards Act. Beef Carcass Grading Regulations. Canada Gazette Part II. 112(13):2945.

AOAC. 1980. Official Methods of Analysis (13th Ed.). Association of Official Analytical Chemists, Washington, DC.

ARC. 1980. The Nutrient Requirements of Ruminant Livestock. Agricultural Research Council. Commonwealth Agricultural Bureaux. Farnham Royal, Slough, England.

Balwin, R.L. and N.E. Smith. 1974. Molecular Control of Energy Metabolism. In: J.D. Sink (Ed.). The Control of Metabolism. p. 17. Pennsylvania State University Press.

Bennett, D.D. and C.C. O'Mary. 1965. Effects of housing vs. open lots on winter gains of beef calves. J. Anim. Sci. 24:854 (Abstr.).

Berger, L.L., S.C. Ricke and G.C. Fahey, Jr. 1981. Alkali treatment of cereal grains. 1. In situ and in vitro evaluation. J. Anim. Sci. 52:138.

Blaxter, K.L. and A.W. Boyne. 1978. The estimation of the nutritive value of feeds as energy sources for ruminants and the derivation of feeding systems. J. Agr. Sci. (Camb.) 90:47.

Blaxter, K.L. and J.L. Clapperton. 1965. Prediction of the amount of methane produced by ruminants. Brit. J. Nutr. 19:511.

Blaxter, K.L., J.L. Clapperton and F.W. Wainman. 1966. Utilization of the energy and protein of the same diet by cattle of different ages. J. Agr. Sci. (Camb.). 63:113.

Brouwer, E. 1965. Report of sub-committee on constants and factors. In: K.L. Blaxter (Ed.) Proc 3rd Symp. Energy Metab. Eur. Assoc. Anim. Prod. Pub. No. 11. pp. 441-443. Academic Press, London.

Byers, F.M. 1980. Determining the effect of monensin on the energy value of corn silage diets for beef cattle by linear or semilog methods. 51:158.

Byers, F.M. 1982. Protein growth and turnover in cattle: Systems for measurements and biological limits. In: F.N. Owens (Ed.) Protein Requirements for Cattle. Division of Agriculture, Oklahoma State Univ. Res. Pub. MP-101. p. 141.

Callow, E.H. 1961. Comparative studies of meat. VII. A comparison between Hereford, Dairy Shorthorn and Friesian steers on four levels of nutrition. J. Agr. Sci. 56:265.

Christopherson, R.J. 1976. Effects of prolonged cold and the outdoor winter environment on apparent digestibility in sheep and cattle. Can. J. Anim. Sci. 56:201.

Christopherson, R.J. 1985. Management and housing of animals in cold environments. In: M.K. Yousef (Ed.) Stress Physiology in Livestock, Vol. 1, Basic Principles, CRC Press, Boca Raton.

Christopherson, R.J. and J.R. Thompson. 1983. Endocrine responses of young bulls kept outdoors during winter. Can. J. Anim. Sci. 63:1019.

Christopherson, R.J, and B.A. Young. 1986. Effects of cold environments on domestic animals. In: O. Gudmundsson (Ed.) Grazing Research in Northern Latitudes. Plenum Publishing Corp., New York.

Christopherson, R.J., J.R. Thompson, V.A. Hammond and G.A. Hills. 1978. Effects of thyroid status on plasma adrenaline and noradrenaline concentrations in sheep during acute and chronic cold exposure. Can. J. Physiol. Pharmacol. 56:490.

Colditz, P.J. and R.C. Kellaway. 1972. The effect of diet and heat stress on feed intake, growth and N-metabolism in Fresian, Brahman x Fresian and Brahman hifers. Aust. J. Agric. Res. 23:717.

Elam, C.J. 1970. Problems related to intensive indoor and outdoor beef production systems. J. Anim. Sci. 32:554.

Environment Canada. 1980. Atmospheric Environment Service. Ottawa, Ontario.

Flatt, W.P., P.W. Moe and L.A. Moore. 1969. Influence of pregnancy and ration composition on energy utilization in dairy cows. In: K.L. Blaxter, J. Kielanowski and G. Thorbec (Eds.) Energy Metabolism of Farm Animals. Eur. Assoc. Anim. Prod. Pub. No. 12. pp. 235. Oriel Press, Newcastle-Upon-Tyne.

Garrett, W.N. 1980a. Energy utilization of growing cattle as determined in seventy-two comparative slaughter experiments. In: L.E. Mount (Ed.) Energy Metabolism. p. 3, EAAP Publ. No. 26. Butterworths, London.

Garrett, W.N. 1980b. Factors influencing energetic efficiency of beef production. J. Anim. Sci. 51:1434.

Garrett, W.N. and N. Hinman. 1969. Re-evaluation of the relationship between carcass density and body composition of beef steers. J. Anim. Sci. 28:1.

Garrett, W.N. and D.E. Johnson. 1983. Nutritional energetics of ruminants. J. Anim. Sci. 57:478.

Geay, Y. 1984. Energy and protein utilization in growing cattle. J. Anim. Sci. 58:766.

Graham, A.D. and R.J. Christopheson. 1981. Effects of adrenaline and noradrenaline on the heat production of warnand cold-acclimated sheep. Can. J. Physiol. Pharmacol. 59:985.

Gregg, V.A. and L.P. Milligan. 1982. Role of Na^+, K^+-ATPase in muscular energy expenditure of warm- and cold-exposed sheep. Can. J. Anim. Sci. 62:123.

Henrickson, R.L., L.S. Pope and R.F. Hendrickson. 1965. Effect of rate of gain of fattening beef calves on carcass composition. J. Anim. Sci. 24:507.

Hidiroglou, M. and J.R. Lessard. 1971. Some effects of fluctuating low ambient temperatures on beef cattle. Can. J. Anim. Sci. 51:111.

Hiner, R.L. and J. Bond. 1971. Growth of muscle and fat in beef steers from 6 to 36 months of age. J. Anim. Sci. 32:225.

Johnson, D.E. and J.C. Crownover. 1975. Energy requirements of feedlot cattle in north central Colorado: Variation in maintenance requirements by month. Research Highlights of the Animal Sciences Department. General Series 948. Colorado State Univ., Fort Collins. pp. 46-49.

Kennedy, P.M. 1985. Influences of cold exposure on digestion of organic matter, rates of passage of digesta in the gastrointestional tract, and feeding and rumination behavior in sheep given four diets in the chopped, or ground and pelleted form. Br. J. Nutr. 53:159.

Kennedy, P.M. and L.P. Milligan. 1978. Effects of cold exposure on digestion, microbial synthesis and nitrogen transformations in sheep. Br. J. Nutr. 39:105.

Kennedy, P.M., R.J. Christopherson and L.P. Milligan. 1976. The effect of cold exposure of sheep on digestion, runen turnover time and efficiency of microbial synthesis. Br. J. Nutr. 36:231.

Kennedy, P.M., R.J. Christopherson and L.P. Milligan. 1982. Effect of cold exposure on feed protein degradation, microbial protein synthesis and transfer of plasma urea to the rumen of sheep. Br. J. Nutr. 47:521.

Kennedy, P.M., B.A. Young and R.J. Christopherson. 1977. Studies on the relationship between thyroid function, cold acclimation and retention time of digesta in sheep. J. Anim. Sci. 45:1084.

Knox, K.L. and T.M. Handley. 1973. The California net energy system. Theory and Application. J. Anim. Sci. 37:190.

Lofgreen, G.P. and W.N. Garrett. 1968. A system for expressing net energy requirements and feed values for growing and finishing beef cattle. J. Anim. Sci. 27:793.

Martin, C.R. 1976. Textbook of Endocrine Physiology. Oxford Univ. Press, New York.

McBride, G.E. 1982. The influence of cold exposure on lactation and growth in sheep. M.Sc. Thesis, The University of Alberta, Edmonton.

Milligan, J.D. and G.I. Christison. 1974. Effects of severe winter conditions on performance of feedlot steers. Can. J. Anim. Sci. 54:605.

Moe, P.W. and H.F. Tyrrell. 1973. The rationale of various energy systems for ruminants. J. Anim. Sci. 37:183.

Muhamad, Y.B., M.P. Hoffman and H.L. Self. 1983. Influence of different ratios of corn and corn silage, housing systems and seasons on the performance of feedlot steers. J. Anim. Sci. 56:747. Nicholson, J.W.G., R.E. McQueen and P.L. Burgess. 1980. Effect of cold on digestibility of chopped or pelleted hay by sheep. Can. J. Anim. Sci. 60:571 (Abstr.).

Nicholson, J.W.G., R.E. McQueen and P.L. Burgess. 1980. Effect of cold on digestibility of chopped or pelleted hay by sheep. Can. J. Anim. Sci. 60:571.

Nour, A.Y.M., M.L. Thonney, J.R. Stouffer and W.R.C. White, Jr. 1981. Muscle, fat and bone in serially slaughtered large dairy or small beef cattle fed corn or corn silage diets in one of two locations. J. Anim. Sci. 52:512.

NRC. 1984. Nutrient Requirements of Domestic Animals. No. 4. Nutrient Requirements of Beef Cattle. Sixth Revised Ed. National Academy of Sciences, Washington, D.C.

Old, C.A. and W.N. Garrett. 1985. Efficiency of feed energy utilization for protein and fat gain in Hereford and Charolais steers. J. Anim. Sci. 60:766.

Sasaki, Y. and T.E.C. Weekes. 1986. Metabolic responses to cold. In: Milligan, L.P., W.L. Grovum and A. Dobson (Eds.) Control of Digestion and Metabolism in Ruminants. pp. 326-343. Reston Publishing Co., Reston.

Slee, J. 1971. Physiological factors affecting the energy cost of cold exposure. Proc. Nutr. Soc. 30:216.

Steel, R.G.D. and J.H. Torrie. 1980. Principles and Procedures of Statistics. A Biometrical Approach. (2nd Ed.). McGraw-Hill Book Co., New York.

Suleiman, A. and G.W. Mathison. 1979. Net energy evaluation of barley diets for cattle in cold environments. J. Anim. Sci. 48:1447.

Thivend, P. and M. Vermorel. 1971. Digestive utilization of starch by the growing lamb. Ann. Biol. Anim. Biochem. Biophys. 11:292.

Tyrell, H.F. and P.W. Moe. 1974. Net energy value of a corn and a barley ration for lactation. J. Dairy Sci. 57:451.

Tyrell, H.F. and P.W. Moe. 1975. Effect of intake on digestive efficiency. J. Dairy Sci. 58:1151.

Van Es, A.J.H. 1978. Nutritional efficiency of protein and fat deposition. In: H. de Boer and J. Martin (Eds.) Patterns of Growth and Development in Cattle. p. 361. Martinus Nijhoff, The Hague.

Van Es, A.J.H. and Y. van der Honing. 1979. Energy utilization. In: W.H. Broster and H. Swan (Eds.) Feeding Strategy for the High Yielding Dairy Cow. pp. 68-89. Granada Publishing, London.

Van Soest, P.J. 1982. Nutritional Ecology of the Ruminant. O. and B. Books, Corvallis.

Waldo, D.R. 1978. Extent and partition of cereal grain starch digestion in ruminants. J. Anim. Sci. 37:1062.

Warren, W.P., F.A. Martz, H.K. Asay, E.S. Hilderbrand, C.G. Payne and J.R. Vogt. 1974. Digestibility and rate of passage by steers fed tall fescue, alfalfa and orchard grass hay in 18 and 32 C ambient temperatures. J. Anim. Sci. 39:93.

Webster, A.J.F. 1970. Direct effects of cold weather on the energetic efficiency of beef production in different regions of Canada. Can. J. Anim. Sci. 50:563.

Webster, A.J.F., J. Chlumecky and B.A. Young. 1970. Effects of cold environments on the energy exchanges of young beef cattle. Can. J. Anim. Sci. 50:80.

Westra, R. and R.J. Christopherson. 1976. Effects of cold on digestibility, retention time of digesta, reticulum motility and thyroid hormones in sheep. Can. J. Anim. Sci. 56:699.

Young, B.A. 1975a. Temperature induced changes in metabolism and body weight of cattle (*Bos taurus*). Can. J. Physiol. Pharmacol. 53:947.

Young, B.A. 1975b. Effects of winter acclimatization on resting metabolism of beef cows. Can. J. Anim. Sci. 55:619.

Young, B.A. 1981. Cold stress as it affects animal production. J. Anim. Sci. 52:154.

Young, B.A. and R.J. Christopherson. 1974. Effect of prolonged cold exposure on digestion and metabolism in ruminants. In: Livestock Environment. p. 75. Proceedings of the International Livestock Environment Symposium. ASAE, St. Joseph, MO.

Young, B.A. and A.A. Degan. 1981. Thermal influences on ruminants. In: J.H. Clark (Ed.) Environmental Aspects of Housing for Animal Production. p. 167. Butterworths, London.

TABLE IV.1. EXPERIMENTAL DIET.

Item	IFN	% of diet
Ingredients[a]		
Barley, dry rolled	4-00-549	94.3
Molasses, wet beet	4-00-668	2.5
Calcium carbonate, 38% Ca	6-01-069	1.3
Urea, 45% N	5-05-070	1.0
Calcium phosphate, 15-18% Ca; 21% P	6-01-082	0.2
Calcium sulfate, 22% Ca; 20% S	6-01-089	0.2
Trace mineralized salt[b]		0.25
Vitamin premix[c]		0.25
Composition, %		
Dry matter		91.7
Crude protein[d]		14.3

[a] Air dry basis.

[b] Trace mineralized salt contained 96.5% NaCl; 0.4% Zn; 0.16% Fe; 0.12% Mn; 0.033% Cu; 0.007% I; 0.004% Co.

[c] Vitamin premix provided 5000 IU Vitamin A; 825 IU Vitamin D and 5 IU Vitamin E per kg total diet.

[d] Dry matter basis.

TABLE IV.2. EFFECT OF LEVEL OF INTAKE ON ENERGY LOSSES AND DIGESTIBLE AND METABOLIZABLE ENERGY VALUES OF THE COMPLETE DIET AND BARLEY GRAIN.

Item	Feeding level, g DM·kg$^{-.75}$·d^{-1} 54	82	SE[a]
No. observations	4	4	
Intake energy, Mcal·d^{-1}	21.7[d]	31.8[e]	.45
Fecal energy, Mcal·d^{-1}	4.18[f]	6.26[g]	.47
Urine energy, Mcal·d^{-1}	1.54	1.55	.41
Methane energy, Mcal·d^{-1}	1.52	1.77	.05
Energy losses, % of IE[b]			
Feces	19.22	19.64	.11
Urine	7.42[f]	4.97[g]	1.61
Methane	6.97[f]	5.65[g]	.15
Energy losses, % of DE			
Urine	9.17[f]	6.13[g]	1.92
Methane	8.63[f]	7.03[g]	.08
Digestible energy, Mcal · kg DM^{-1}			
Complete diet	3.39	3.38	.06
Barley[c]	3.48	3.46	.08
Metabolizable energy, Mcal · kg DM^{-1}			
Complete diet	2.79	2.93	.06
Barley[c]	2.85	3.04	.07
ME/DE in complete diet, %	82.2	86.8	1.21

[a] Standard error.

[b] Combustible energy intake.

[c] Energy values for barley grain were calculated assuming that molasses provided 3.48 and 2.86 Mcal of DE and ME·kg^{-1} DM, respectively (NRC, 1984).

[de] Means in the same row with different superscripts are significantly different (P<.001).

[fg] Means in the same row with different superscripts are significantly different (P<.05).

TABLE IV.3. MEAN, MEAN MAXIMUM AND MINIMUM TEMPERATURES, NUMBER OF DAYS THE MEAN OUTDOOR TEMPERATURE WAS BELOW -20 C AND RELATIVE HUMIDITY DURING THE FEEDING PERIOD.

Item	Month of experiment				Overall
	January	February	March	April	
Days on feed	22	29	31	18	
Indoor group					
Mean temperature, C	15.2 ± 3.5[a]	15.7 ± 2.0	18.2 ± 3.1	18.9 ± 1.1	16.9 ± 2.7
Relative humidity, %	74.0 ± 6.4	79.0 ± 5.0	76.0 ± 3.7	76.0 ± 2.6	76.4 ± 4.7
Outdoor group					
Mean temperature, C	-14.8 ± 9.4	-10.2 ± 5.6	-7.2 ± 6.4	4.7 ± 4.7	-7.6 ± 6.8
Mean maximum temperature, C	-9.6 ± 9.5	-4.2 ± 5.7	-1.3 ± 5.7	11.3 ± 6.5	-1.7 ± 6.8
Mean minimum temperature, C	-20.4 ± 9.1	-16.2 ± 5.7	-13.1 ± 7.4	-2.2 ± 3.7	-13.6 ± 6.9
Days mean temperature below -20 C	7	0	2	0	9
Relative humidity, %	68.0 ± 6.7	75.0 ± 7.4	67.0 ± 7.8	66.0 ±13.9	69.4 ± 8.9

[a]Mean ± standard deviation.

TABLE IV.4. EFFECT OF FEEDING LEVEL AND LOCATION (INDOOR OR OUTDOOR) ON FEEDLOT PERFORMANCE OF STEERS.

Item	Feeding level[a]			Location Mean	SE[b]	
	Low	Medium	High		Location	Level
No. steers						
Indoor	7	7	5	19		
Outdoor	7	7	6	20		
Dry matter intake, $g \cdot kg^{-.75} \cdot d^{-1}$						
Indoor[dh]	51.6	64.3	69.3	60.9	.47	.58
Outdoor[dj]	52.8	64.8	70.3	62.2		
Mean[dk]	52.2	64.5	69.9			
Metabolizable energy intake[c], $kcal \cdot kg^{-.75} \cdot d^{-1}$						
Indoor[dh]	141	180	199	171	1.4	1.6
Outdoor[dj]	144	181	202	174		
Mean[dk]	142	181	201			
Initial weight, kg						
Indoor	341	328	329	333[m]	4.3	5.3
Outdoor	350	349	344	348		
Mean	345	339	337			
Final weight, kg						
Indoor[e]	381	403	420	400	4.4	5.4
Outdoor[g]	377	400	401	393		
Mean[g]	379	402	410			
Average daily gain, g						
Indoor[d]	410	750	920	670[l]	20	30
Outdoor[dk]	280	510	570	450		
Mean[dk]	340	630	730			
Gain:Feed, $g \cdot kg^{-1}$						
Indoor[d]	91	134	150	122[m]	4	6
Outdoor[g]	62	90	93	81		
Mean[e]	77	112	119			

[a] 52, 64 and 70 g DM $\cdot kg^{-.75} \cdot d^{-1}$ for low, medium and high; respectively.
[b] Standard error of mean.
[c] Estimated using average ME obtained in a thermoneutral environment with steers consuming the experimental diet.
[defg] Linear feeding level effect (P<.001), (P<.005), (P<.05) and (P<.1); respectively.
[gijk] Quadratic feeding level effect (P<.001), (P<.005), (P<.05) and (P<.1); respectively.
[lm] Indoor different from outdoor (P<.001) and (P<.05); respectively.

TABLE IV.5. EFFECT OF FEEDING LEVEL AND LOCATION (INDOOR OR OUTDOOR) ON CARCASS CHARACTERISTICS OF STEERS.

Item	Feeding level[a]			Location Mean	SE[b]	
	Low	Medium	High		Location	Level
No. steers						
Indoor	7	7	5	19		
Outdoor	7	7	6	20		
Warm carcass weight, kg						
Indoor[e]	221	233	238	230[i]	2.9	3.5
Outdoor[ch]	204	222	222	216		
Mean[cf]	213	227	229			
Dressing percentage						
Indoor	58.0	57.6	56.8	57.5[i]	.33	.4
Outdoor	54.0	55.5	55.3	54.9		
Mean	56.0	56.6	56.0			
Fat depth, mm						
Indoor[e]	7.9	8.6	12.1	9.3[i]	.49	.6
Outdoor[dg]	4.1	7.6	6.6	6.1		
Mean[g]	6.0	8.1	9.1			
Rib-eye area, cm^2						
Indoor	60.4	62.7	62.6	61.8	1.1	1.4
Outdoor[eh]	59.2	63.3	61.5	61.4		
Mean	59.8	63.0	62.0			

[a] 52, 64 and 70 g DM·$kg^{-.75}$·d^{-1} for low, medium and high; respectively.

[b] Standard error of mean.

[cde] Linear feeding level effect (P<.001), (P<.01) and (P<.05); respectively.

[fgh] Quadratic feeding level effect (P<.001), (P<.005) and (P<.05); respectively.

[i] Indoor different from outdoor (P<.001).

TABLE IV.6. EFFECT OF FEEDING LEVEL AND LOCATION (INDOOR OR OUTDOOR) ON FINAL EMPTY BODY COMPOSITION.

Item	Feeding level[a]			Location Mean	SE[b]	
	Low	Medium	High		Location	Level
No. steers						
Indoor	7	7	5	19		
Outdoor	7	7	6	20		
Carcass specific gravity						
Indoor	1.070	1.068	1.065	1.068[f]	.001	.001
Outdoor	1.078	1.074	1.074	1.076		
Mean	1.074	1.071	1.070			
Empty body weight, kg						
Indoor[d]	330	347	355	343[g]	4.0	4.8
Outdoor[d]	308	333	332	324		
Mean[c]	320	340	343			
Empty body fat, kg						
Indoor	59.0	67.0	73.0	65.6[f]	2.8	3.4
Outdoor[e]	42.4	52.4	53.6	49.2		
Mean[e]	50.7	59.7	62.4			
Empty body protein, kg						
Indoor	60.3	62.3	63.0	61.7	.89	1.1
Outdoor	58.8	62.2	61.9	60.9		
Mean[e]	59.6	62.3	62.4			
Empty body energy, Mcal						
Indoor[e]	880	965	1026	950[f]	25.7	30.7
Outdoor[d]	713	827	836	790		
Mean[d]	797	896	922			

[a] 52, 64 and 70 g DM·kg$^{-.75}$·d^{-1} for low, medium and high; respectivily.

[b] Standard error of mean.

[cde] Linear feeding level effect (P<.005), (P<.05) and (P<.1); respectively.

[fg] Indoor different from outdoor (P<.001) and (P<.005); respectively.

TABLE IV.7. EFFECT OF FEEDING LEVEL AND LOCATION (INDOOR OR OUTDOOR) ON EMPTY BODY GAIN.

Item	Feeding level[a]			Location	SE[b]	
	Low	Medium	High	Mean	Location	Level
No. steers						
Indoor	7	7	5	19		
Outdoor	7	7	6	20		
Weight, $g \cdot kg^{-.75} \cdot d^{-1}$						
Indoor[cg]	4.7	7.8	8.6	6.9[i]	.25	.3
Outdoor[cg]	1.0	4.0	4.5	3.1		
Mean[ch]	2.9	5.9	6.3			
Protein, $kcal \cdot kg^{-.75} \cdot d^{-1}$						
Indoor	3.1	5.5	5.8	4.7[j]	.43	.52
Outdoor[e]	1.0	3.3	3.6	2.6		
Mean[dh]	2.0	4.4	4.6			
Fat, $kcal \cdot kg^{-.75} \cdot d^{-1}$						
Indoor[f]	22.1	31.5	38.9	30.0[i]	3.0	3.6
Outdoor[e]	1.2	12.9	14.9	9.6		
Mean[e]	12.0	22.2	25.8			
Energy, $kcal \cdot kg^{-.75} \cdot d^{-1}$						
Indoor[e]	25.3	37.2	44.9	34.8[i]	2.7	3.3
Outdoor[d]	2.9	16.2	18.5	12.3		
Mean[g]	14.1	26.7	30.5			

[a] 52, 64 and 70 g DM$\cdot kg^{-.75} \cdot d^{-1}$ for low, medium and high; respectivily.

[b] Standard error of mean.

[cdef] Linear feeding level effect (P<.001),(P<.005), (P<.05) and (P<.1); respectively.

[gh] Quadratic feeding level effect (P<.05) and (P<.1); respectively.

[ij] Indoor different from outdoor (P<.001) and (P<.005); respectively.

TABLE IV.8. MAINTENANCE REQUIREMENTS, EFFICIENCY OF ENERGY USE AND NET ENERGY CONTENT OF THE ALL-CONCENTRATE DIET AND BARLEY GRAIN AS INFLUENCED BY ENVIRONMENT.[a]

Item	Indoor[b]	Outdoor[c]
No. steers	21	21
Maintenance requirements		
Metabolizable energy, kcal·kg$^{-.75}$·d^{-1}	101	142 **
Dry matter, g·kg$^{-.75}$·d^{-1}	35.2	49.5 **
NEm, kcal·kg$^{-.75}$·d^{-1}	64.8	76.2 **
Efficiency of ME utilization, %		
Maintenance, km	.64	.55
Gain, kf	.45	.27
Protein gain	12.8	11.4
Fat gain	90.9	71.4
Net energy values		
Complete diet		
NEm, Mcal·kg dry matter^{-1}	1.84	1.54
NEg, Mcal·kg dry matter^{-1}	1.29	0.76
Barley		
NEm, Mcal·kg dry matter^{-1}	1.96	1.64
NEg, mcal·kg dry matter^{-1}	1.37	0.81

[a] Values for efficiency of ME use for protein and fat gain were estimated by multiple regression (Old and Garrett, 1985), NEg values were estimated by linear regression of retained energy on DM intake and all other values were estimated from the regression of log HE vs ME intake (Lofgreen and Garrett, 1968).

[b] Regressions for the indoor group are as follows:

log HE = 1.8119 + .0019(ME), r = 0.71, standard error of estimate = 0.04, (P<.001).

ME intake = 103.66 + 7.82(PROTEIN) + 1.07(FAT), r = 0.82, standard error of estimate = 14.2, (P<.001).

RE = -35.22 + 1.29(DM), r = 0.55, standard error of estimate = 13.1, (P<.05).

[c] Regressions for the outdoor group are as follows:

log HE = 1.882 + .0019(ME), r = 0.90, standard error of estimate = 0.02, (P<.001).

ME intake = 140.29 + 8.79(PROTEIN) + 1.42(FAT), r = 0.77, standard error of estimate = 19.5, (P<.001).

RE = -49.47 + 0.76(DM), r = 0.53, standard error of estimate = 10.0, (P<.05).

** Means in the same row are significantly different (P<.01).

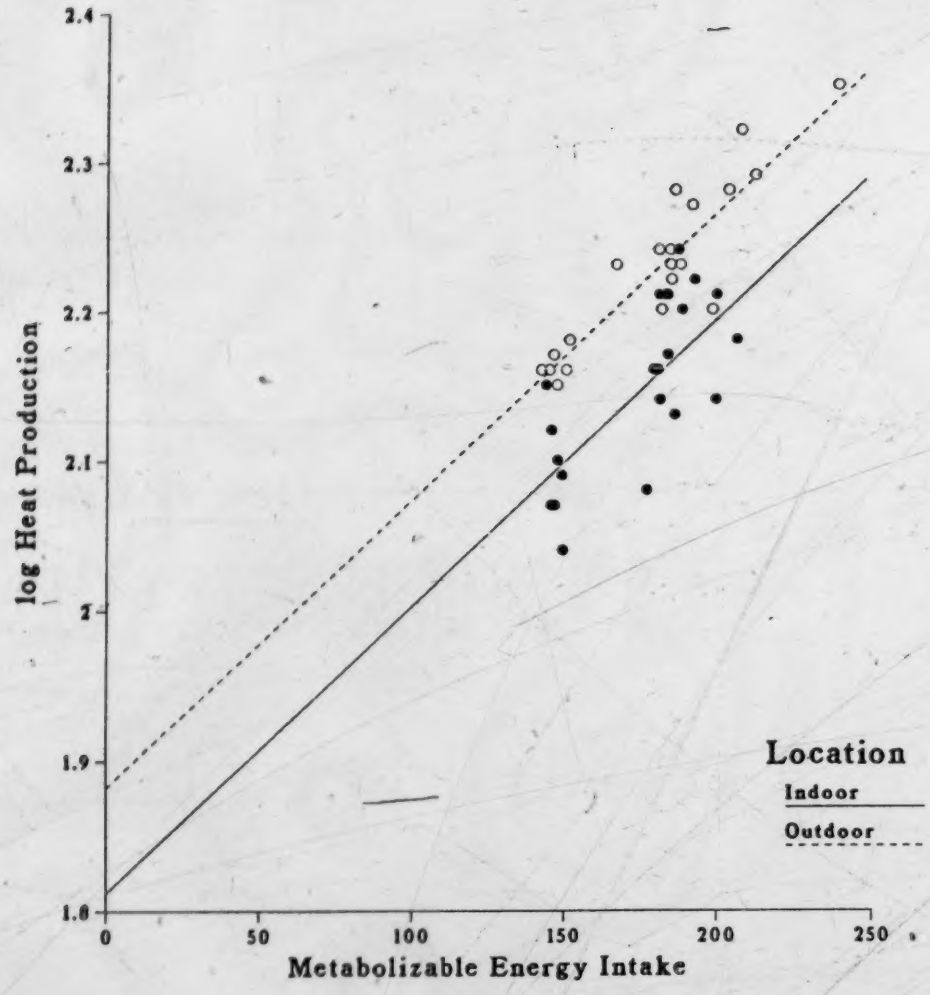

Figure IV.1 Relationship between log heat production ($kcal \cdot kg^{-.75} \cdot d^{-1}$) and metabolizable energy intake ($kcal \cdot kg^{-.75} \cdot d^{-1}$) for indoor and outdoor steers.

V. GENERAL DISCUSSION AND CONCLUSIONS.

The results of the experiments in Chapter III of this thesis demonstrate that lasalocid tended to improve the performance of feedlot cattle fed a high-concentrate barley-based diet. Overall lasalocid resulted in a 10% increase in average daily gain and a 9% increase in feed efficiency. This effect was caused mainly by an improvement in the ME content of the diet. It is also apparent from these experiments that lasalocid influenced the partitioning of dietary ME between maintenance and growth. Cattle fed the diet containing lasalocid had slightly higher fasting heat productions however because of the improved dietary ME, the amount of DM required to meet the maintenance requirement was reduced. Thus at equal DM intakes the animals consuming the lasalocid supplemented diet had more ME available for growth. Lasalocid did not influence the partitioning of ME above maintenance.

The dramatic effect of a cold environment on the performance of feedlot cattle is clearly illustrated in Chapter IV. One of the main causes of the reduced performance in the cold exposed cattle in this experiment was an apparent substantial increase in resting metabolic rate. Considerably more energy was used for maintenance, thus at equal DM intakes less ME was available for growth. Cold exposure also influenced the partitioning of energy for growth in the outdoor animals by increasing the relative proportions of dietary energy going to the less efficient

process of protein deposition. Overall the effects of cold resulted in a 33% decline in average daily gain and a 34% reduction in feed efficiency of the outdoor steers.

Few reports are available in the literature in which the combined effects of cold and ionophore supplementation on animal performance have been studied. Meiske et al. (1977) and Smith et al. (1977) investigated the response to monensin of cattle fed with or without shelter during the winter in Minnesota. These authors reported that feeding monensin resulted in reduced feed intake, increased average daily gain and improved feed efficiency for cattle fed in open lots or in warm confinement barns. Housing environment did not influence the percentage response to monensin for any of the variables measured, indicating that the beneficial response to the ionophore in the cold was similar in magnitude to the response in the warm. However, the performance of the outside group supplemented with monensin was less than that of the control, warm confinement, group. This indicates that, although monensin improved animal performance in the cold, the response was not sufficient to offset the negative effects of cold. In view of the very large decline in performance of the cold exposed cattle reported herein, it is doubtful that ionophore supplementation, when energy was limiting, would have resulted in a similar performance of animals in cold environments as that achieved in warm environments. A similar conclusion was reached by Horton (1981) who reported

that, although monensin enhanced the efficiency of ruminal fermentation, it did not appear to increase the ability of sheep to withstand the effects of cold exposure.

The California Net Energy System (CNES) is the major net energy system for ruminants currently in use in North America. The National Research Council has included NEm and NEg values in their Beef and Dairy Cattle Nutrient Requirements publications since 1970 and 1971, respectively. Information gained in these studies casts serious doubt on the validity of net energy values obtained in the CNES and on the application of these values to different production situations.

In estimating dietary NE values with the CNES, it is common practice to use an average dietary ME value for the feed rather than actual ME values obtained at different intakes (Garrett, 1976; Lofgreen, 1976; Byers, 1980; Wedegaertner and Johnson, 1983). In Chapter III it was clearly shown that using one ME value would lead to large errors in kf and subsequently NEg. If the single ME value was determined at maintenance intake, the estimated kf would normally be smaller than the same value estimated using a dietary ME content determined at a high feeding level. The results of the experiments reported in Chapter III indicate that the most accurate estimate of kf and thus NEg would be to use ME values actually obtained at each feeding level, thus the influence of feed intake on dietary ME content would be accounted for.

The current concept of applying a single net energy value to feeds, as is the case with the CNES, and using this value to predict animal performance under all production situations is questionable. In Chapter IV it was demonstrated that the NEg value determined for the diet in a thermoneutral environment was similar to the NEg value estimated from the equation relating ME to NEg used by the NRC (1984). However, the NEg value determined for the same diet in a cold environment was about 40% less. This difference could not be accounted for by differences in fecal, urinary and gaseous losses. This is conclusive evidence that a single net energy value determined for a diet under specific conditions cannot be applied across all production situations.

The efficiency with which ME is used for growth, kf, has been considered to be mainly a function of the ME content of the diet (ARC, 1980; NRC, 1984). It has been well established, however, that the type of tissue being deposited in the growing animal will have a major effect on kf. The efficiency of ME use for protein deposition has been estimated to be between five and nine times less efficient than fat deposition. Physiological and environmental factors are known to influence the type of tissue being deposited in the growing animal. Thus these factors will have an effect on kf and subsequently on the estimated net energy value of a diet. Therefore in order for a feed evaluation system to be most useful it should

incorporate the animal's physiological and environmental states in predicting the value of a feed for promoting growth. Overall, then, the results of these studies suggest that a more flexible system for feed energy is needed before it will be useful under many production conditions.

A. BIBLIOGRAPHY

ARC. 1980. The Nutrient Rquirements of Ruminant Livestock. Agriculture Research Council. Commonwealth Agricultural Bureaux. Farnham Royal, Slough, England.

Byers, F.M. 1980. Determining effects of monensin on energy values of corn silage diets for beef cattle by linear or semi-log methods. J. Anim. Sci. 51:158.

Garrett, W.N. 1976. Influence of rumensin on energy utilization of corn and barley diets. 15th Annu. California Feeders Day 21:27.

Horton, G.M.J. 1981. Manipulating energy metabolism in sheep exposed to cold. Am. J. Vet. Res. 42:146.

Lofgreen, G.P. 1976. A comparison of sodium bicarbonate with rumensin in a finishing ration. 15th Annu. California Feeders Day 15:20.

Meiske, J.C., R.D. Goodrich, J.A. Moore and R.L. Larson. 1977. Effect of monensin as influenced by housing system. Minnesota Cattle Feeder's Rep. B-226.

NRC. 1984. Nutrient Requirements of Domestic Animals. No. 4. Nutrient Requirements of Beef Cattle. Sixth Revised Ed. National Academy of Science, Washington, D.C.

Smith, R.E., H.E. Hanke, L.K. Lindor, R.D. Goodrich and J.C. Miske. 1977. Performance of crossbred steers fed rations with or without moninsin in two housing systems. Minnesota Cattle Feeder's Rep. B-228.

Wedegaertner, T.C. and D.E. Johnson. 1983. Monensin effects on digestibility, methanogenesis and heat increment of a cracked corn-silage diet fed to steers. J. Anim. Sci. 57:168.